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# Geohydrology of the Lost Creek Cave System, Park County, Montana

## Abstract

Lost Creek is a tributary of the West Boulder River located in eastern Park County, Montana, and drains a portion of the West Boulder Plateau of the Absaroka-Beartooth Range, a 3,000 m high plateau composed of Precambrian rock. Lost Creek crosses a fault contact between granite and limestone at the northeast edge of the plateau and abruptly plunges into a deep swallow hole. The underlying cave system has been explored to a depth of nearly 245 m. The cave is bedding-plane controlled and follows a thick limestone layer in the upper Madison Group. The Madison Group has been deformed into two folds, the Lion Mountain anticline and the Lion Mountain syncline. Lost Creek Cave is developed in the southwest limb of the syncline. The resurgence of Lost Creek, determined by dye tracing and water chemistry, is located at West Boulder Cave near the West Boulder River.

The Lost Creek area has been actively glaciated. The origin and subsequent development of Lost Creek Cave is probably directly related to the glacial history of the area.

## Introduction

Lost Creek is part of the West Boulder River drainage in eastern Park County, Montana (Fig 1). Lost Creek originates in the West Boulder Plateau of the Absaroka-Beartooth Range and follows a glaciated valley for about 20 k to a point located in the N½, section 12, T4S, R11E where the creek sinks spectacularly into a deep pit (Fig. 2). The underlying cave system (Lost Creek Cave) has been explored to a depth of nearly 245 m. A second cave (West Boulder Cave) in the SW¼, section 2, T4S, R11E, near the West Boulder River, contains a large spring that has long been thought to be the resurgence of Lost Creek. About 1,800 horizontal meters and 335 meters of elevation separate the entrance pit of Lost Creek Cave from the spring of West Boulder Cave.

## Purpose

This study of the Lost Creek Cave system was made in order to locate the true resurgence of Lost Creek and determine the structural control of the cave. The work was also intended to develop criteria for evaluation of other similar groundwater systems that exist around the edge of the Beartooth Plateau and other high mountain regions in Montana and Wyoming.

## Background

The existence of Lost Creek Cave has been known by local ranchers and forest service personnel since the 1930's. Reports of the cave are on file at the U.S. Forest Service station at Livingston, Montana. The cave was first visited by the author in the summer of 1970 as part of the Montana Cave Survey project for the Montana Bureau of Mines and Geology. West Boulder Cave was mapped at that time (Fig. 3). Exploration of Lost Creek Cave was carried out during the winters of 1972 through 1974 and a sketch map down to the 245 m level was completed (Fig. 4). Field work and dye-testing were done in the summers of 1973 and 1974.

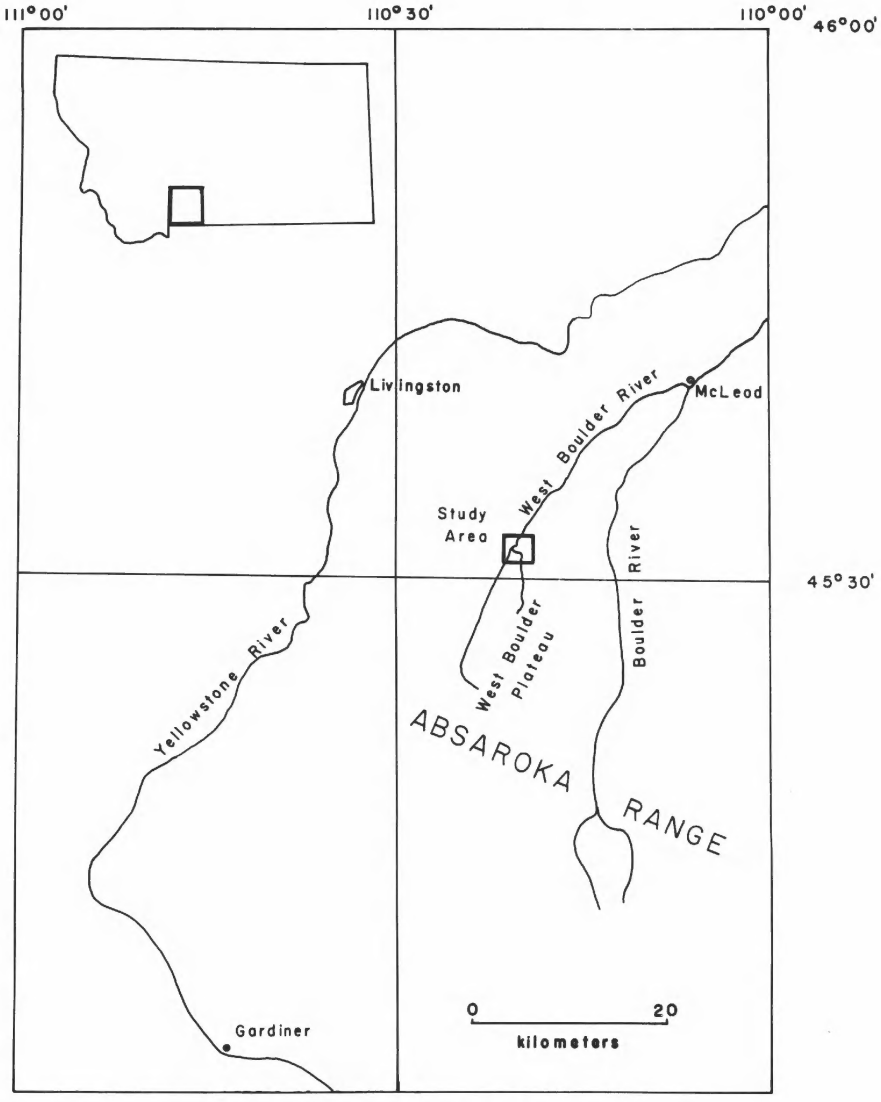


Figure 1. Index map of southcentral Montana showing the study area.

**Geology**

The geology of eastern Park County is described by Richards (1957). Richards' map covers part of the West Boulder Plateau and northern foothills, including the Lost Creek drainage. No mention is made of Lost Creek Cave or West Boulder Cave.

*Stratigraphy*

The only rocks associated with the cave system are Precambrian granites, Mississippian limestone, and Quaternary glacial debris. Precambrian geology in the North Snowy

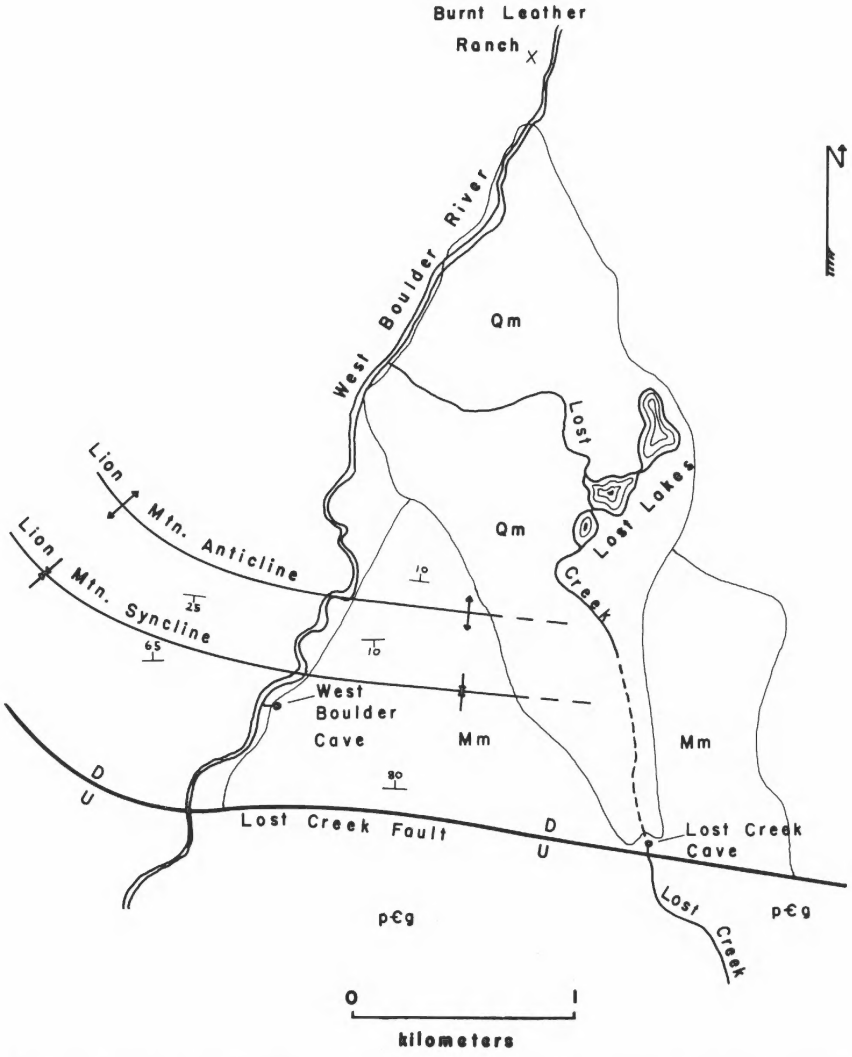


Figure 2. Map of the lower Lost Creek area showing the geology around Lost Creek and West Boulder Cave: pCg = Precambrian granite and gneiss; Mm = Mississippian Mission Canyon Group; Qm = Quaternary glacial moraine (modified after Richards, 1957).

Block, described by Foose and others (1961), is complex. In upper Lost Creek, immediately south of Lost Creek Cave, the rocks are coarse-grained granites. Farther upstream are Precambrian metamorphic rocks—gneiss, schist, and quartzite. These rocks comprise much of the glacial debris found below Lost Creek. Quartz sand found in West Boulder Cave is almost certainly derived from Precambrian rock.

Both Lost Creek Cave and West Boulder Cave are developed in Madison Group carbonates of Mississippian age. The Madison Group is composed of light gray, finely

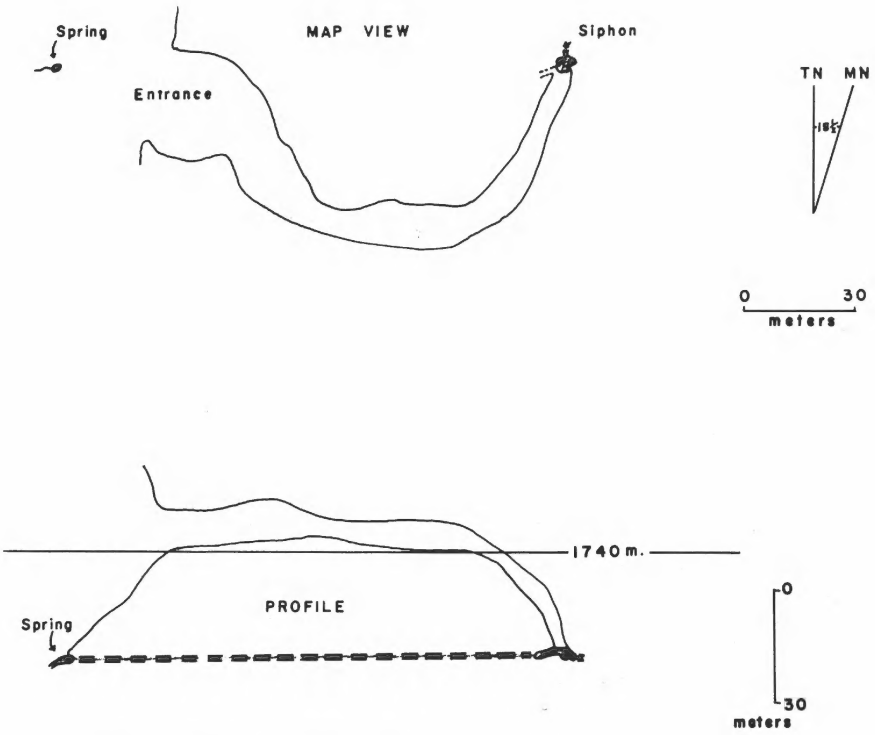


Figure 3. Map and profile of West Boulder Cave.

crystalline, crinoidal limestone containing a few silty layers. The lower 76 m is thin-bedded and cherty (Lodgepole?) while the upper part is massive and partly brecciated (Mission Canyon?). Richards measured 262 m of Madison rocks in the Lost Creek Cave area but was unable to divide them into lower Lodgepole and upper Mission Canyon units. The upper massive zone is similar to the Mission Canyon elsewhere in Montana in that it contains caves and solution pockets. The lower 76 m has few solution features.

Glacial till, consisting primarily of Precambrian debris, covers the floor of Lost Creek Canyon and most of the slope between Lost Creek Cave and West Boulder meadows, including the Lost Lakes depression.

*Structure*

Two features dominate the structure of lower Lost Creek—the Lost Creek fault and the Lion Mountain folds. The West Boulder Plateau of the Absaroka-Beartooth Range has been elevated to a height of 3,000 m by faulting. Along the Lost Creek fault, uplift has placed Precambrian granite in contact with the Madison Group near Lost Creek Cave. The fault plane is nearly vertical at Lost Creek; faulting may have created some drag folding on Madison beds (see Fig. 7 and discussion, page 9). The fault crosses the West Boulder River about 300 m above West Boulder Cave but Lost Creek Cave is within 100 m of the fault.

North and east of the Lost Creek fault, the Madison Group has been folded into an

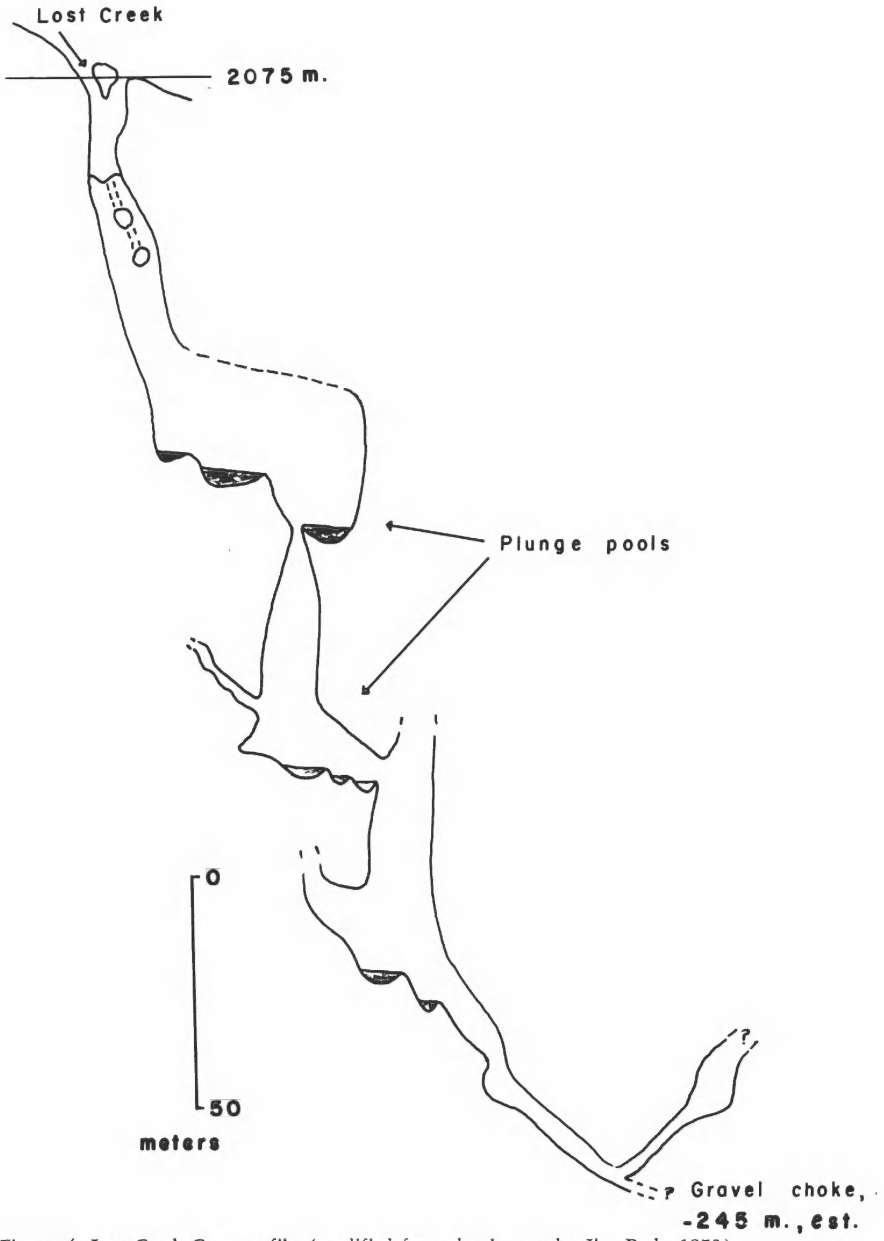


Figure 4. Lost Creek Cave profile (modified from sketch map by Jim Peck, 1973).

anticline and syncline with the syncline nearest the fault (Fig. 2). It is difficult to determine the plunge of the folds but on the West Boulder River, the Lion Mountain anticline appears to plunge southward (Fig. 5). Both West Boulder Cave and Lost Creek Cave

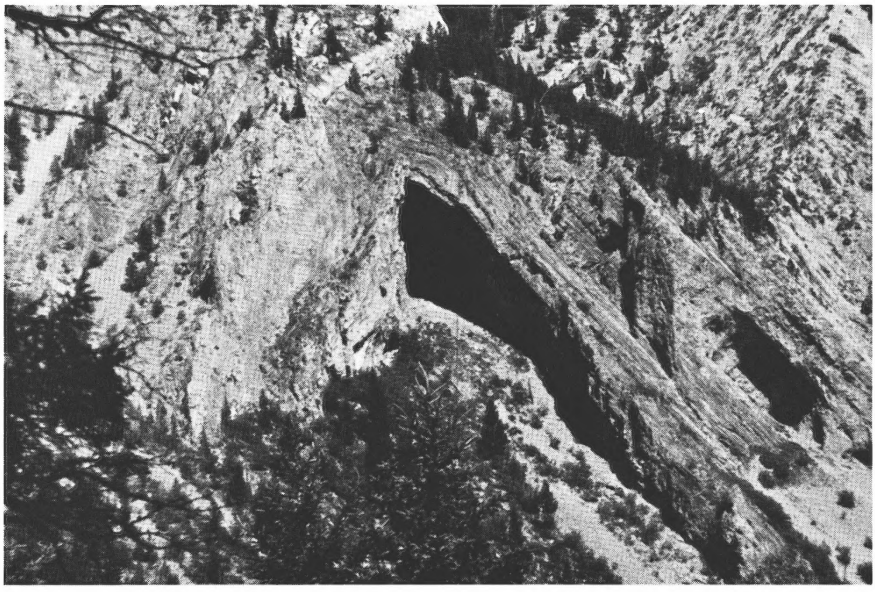

Figure 5. Photo looking northward at the Lion Mountain fold.

are formed in the southwest limb of the Lion Mountain syncline. The dip along this limb of the fold ranges from 35° to 80°.

*Surface Geology*

A distinctive glacial valley extends from upper Lost Creek northward to where Lost Creek fault crosses Lost Creek. Here Lost Creek makes a sharp westward bend and flows parallel to the fault for a distance of about 150 m. The stream then turns northward and continues over Madison limestone for about 100 m and then sinks (Fig. 6). Outcrops along the stream bed clearly expose the fault and limestone.

Below Lost Creek Cave, a dry valley continues northward toward Lost Lake. About 1 km downstream, water reappears in the stream bed from small croppings of Madison rocks. However, the volume of water is much less than that of upper Lost Creek. The water, averaging .02 to .04 cubic meters per second (1-2cfs), flows into Lost Lakes farther downstream.

The entrance to West Boulder Cave lies less than 30 m above the West Boulder River in an east-dipping layer of yellowish-brown, brecciated Madison limestone. Glacial material and stream alluvium cover most of the area surrounding the cave entrance but the Lost Creek fault can be seen crossing the north side of West Boulder Canyon about 400 m upstream from the cave.

**Groundwater Flow System**

*Intake*

Lost Creek flows into a swallow hole about 6 m in diameter. The stream drops for a distance of 25 m and then plunges downward in a series of waterfalls through seven more pits that vary in depth from 6 to 43 m (Fig. 4). At 245 m the stream siphons

into a gravel plug but the cave may continue beyond the siphon, probably at a much flatter gradient.

Lost Creek Valley, below the intake pit, is completely dry for a distance of 1 km. Even during flood stage, all of the Lost Creek water flows underground. There is no indication that excess water has spilled into the dry valley for many years. Apparently the underground conduit is large enough to handle great amounts of runoff.

The discharge of Lost Creek is variable. In June 1971, it was estimated as 22 cubic meters per second (800 cfs), and in February 1972, as 0.6 cubic meters per second (20 cfs).

Two attempts were made in July 1973 to measure the discharge of water flowing into the cave. The stream was extremely low for late July because of one of the driest winters on record. The first method, using cross-sectional measurements and velocity from floating objects, gave a discharge of 1.62 m per second (57.6 cfs). A second more accurate method of determining stream discharge was made with dye, using the procedure outlined by Wilson (1968). Ten ml of 20 percent Rhodamine WT dye were placed in Lost Creek and water samples were collected downstream. The volume of upper Lost Creek was calculated at 1.65 cubic meters per second (58.1 cfs).

*Resurgence*

The resurgence of Lost Creek is now known to be at West Boulder Cave. Other possible outlets originally considered included Lost Lakes, springs and seeps below Lost Lakes, and the main Boulder River. Three attempts were made to locate the true resurgence. The first two attempts were probably unsuccessful because of the short collection time and the small volume of dye used. In March 1974, a third test was made. One liter of dye was injected into Lost Creek Cave and charcoal was left in place for two weeks. A weak but positive test for dye in the charcoal at West Boulder Springs confirmed a connection between the two caves. No dye was recovered at Lost Lakes, other nearby springs, or along the main Boulder River.

Failure to get a strong dye test may be due to flushing of most of the dye from the charcoal or because part of Lost Creek resurges at another location. Flushing of the dye seems more likely as the charcoal lay in the spring outlet for two weeks.

The velocity of Lost Creek plus the high gradient between Lost Creek Cave and the West Boulder River (335 vertical meters) suggest that the dye should have traveled the 1,800 horizontal meters to West Boulder Cave in less than one hour. The long delay in flow through time may be due to pooling of the water. The map of Lost Creek Cave shows plunge pools at the base of each waterfall. These pools are as large as 15 m across and 2 m deep. The dye could have been delayed at each pool long enough to account for the slow travel time. A better test in the future might be to inject the dye at the 245 m level below the last plunge pool or to inject floating material such as dyed lycopodium spores.

Considerations of discharge and water chemistry confirm West Boulder Cave spring as the outlet. The discharge of upper Lost Creek was compared with that of the springs at West Boulder Cave. If the discharge of water flowing from West Boulder Cave springs were greater than that flowing into the swallow hole on Lost Creek, it would indicate that additional water was entering the cave system from another source (such as nearby Grouse Creek which also sinks). On the other hand, if upper Lost Creek feeds springs other than the one at West Boulder Cave, the discharge should be much less.

Tests indicated that the water emerging from West Boulder Cave was of nearly the same volume as that of upper Lost Creek. Analysis of Lost Creek water and West Boulder Cave spring water shows a distinct similarity and will be discussed later.

Other possibilities for the resurgence of Lost Creek can be eliminated. Lost Lakes lie about 2 km down valley from the swallow hole and could be fed by Lost Creek water. The valley, for a distance of 1 km below Lost Creek Cave, is dry during the entire year. The volume of the small stream that flows into Lost Lakes is much less than that of upper Lost Creek and it maintains a steady flow even during spring runoff. The possibility that Lost Creek feeds Lost Lakes through an underground outlet has to be ruled out because the volume of the lakes' outlets is nearly the same as the intake and does not change throughout the year.

A large number of springs flow from the moraine north and west of Lost Lakes, the sum of which could account for the volume of water flowing into the swallow hole. Charcoal was placed at two of the larger springs in the August 1973 and March 1974 tests but no dye was recovered.

The band of Madison limestone containing the caves continues eastward and crosses the main Boulder River about five miles away. Water from Lost Creek could conceivably connect with the main Boulder River near the falls. Charcoal samples placed downstream from Boulder Falls collected no dye during any tests.

*West Boulder Cave*

West Boulder Cave lies 18 m above the West Boulder River and 326 m below Lost Creek Cave. A large spring issues from rocks just below the cave entrance. The cave has been mapped for a distance of 61 m where it siphons at a small pool. The pool varies in depth depending on the season of the year—higher during the spring runoff and lower during the fall and winter months. During low water, another 15 m of passage can be followed beyond the pool.

When visited by Jim Chester in 1972 (pers. comm., November 1973), the pool level was rising and falling at rapid intervals. The pool would drain during an interval of three to fifteen minutes and then refill from two to five minutes later. An ebb and flow spring is uncommon and usually implies multiple entrances to the cave system (Jennings, 1972, p. 77) or air entrapment in large chambers within the cave. A search for other entrances between Lost Creek and West Boulder Caves was unsuccessful. Apparently the pool ebbs and flows only during certain times of the year as two other trips failed to note any changes in water level. Exactly how the ebbing and flowing relates to the groundwater flow system leading to West Boulder Cave is unclear, but the possibility of multiple cave levels, large passages, and other entrances is enhanced by its discovery.

The floor of West Boulder Cave is partially composed of coarse quartz sand, probably derived from Precambrian granite. Much of the sand lies near the back of the cave where it could not have been washed in by surface runoff. Unless the sand was washed in by the West Boulder River during a late stage of downcutting (which seems unlikely), the sand was probably brought in through an underground channel from Lost Creek.

**Geologic Control of the Cave System**

Both Lost Creek Cave and West Boulder Cave lie in the west limb of the Lion Mountain syncline (Fig. 2). Although the Lost Creek fault passes within 100 m of Lost Creek

Cave, the cave is not fault controlled. Lost Creek crosses the fault and 100 m of Madison carbonates before sinking (Fig. 6). If the cave were fault controlled, the stream should have flowed underground somewhere along the granite-limestone contact. No evidence of faulting can be seen anywhere in Lost Creek Cave and it is formed entirely in limestone.

The Madison Group at the fault contact near stream level strikes N80E and dips 63° south, in direct contrast to the north-dipping Madison rock farther downstream. Fault drag has bent the upper part of the Madison so that Lost Creek flows over thin-bedded lower Madison rocks first (Fig. 7). One hundred meters downstream, the stream encounters a massive fossiliferous carbonate unit. The thin-bedded units probably represent the Lodgepole member of the Madison Group and the thick, massive bed is part of the Mission Canyon member. In other locations in Montana, the Mission Canyon contains numerous caves while the thin-bedded Lodgepole rarely develops caves.

Within Lost Creek Cave, passages are largely controlled by bedding planes. The cave is formed in a single massive limestone bed which at first dips steeply south, then becomes vertical and finally dips northward. It is this bedding-plane configuration, the result of a fault drag on the syncline limb, that gives Lost Creek Cave its vertical nature.

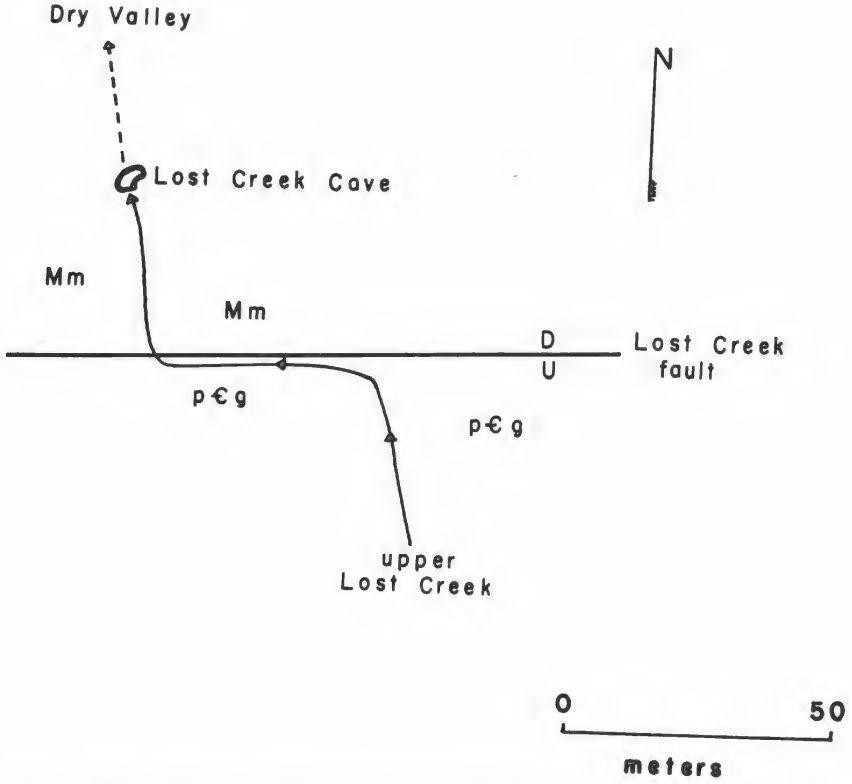


Figure 6. Sketch map of the area around Lost Creek Cave: pCg = Precambrian granite and gneiss; Mm = Mississippian Madison Group.

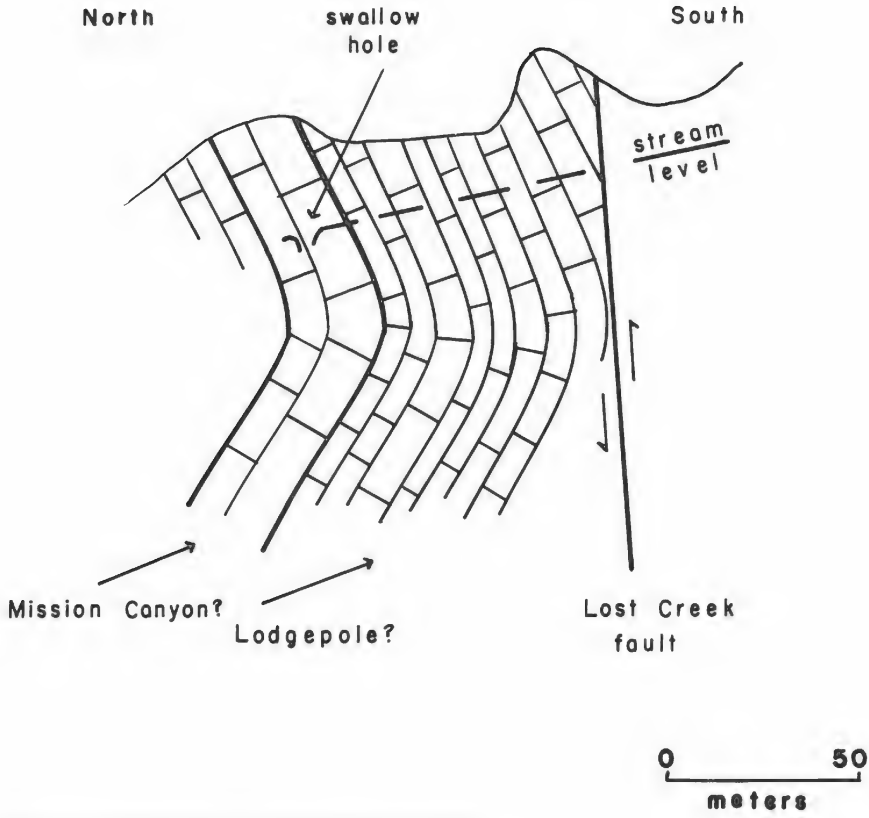


Figure 7. Profile sketch of the Lost Creek Cave area.

Beyond the 245 m level in the cave, one can make a reasonable guess about the passage profile. West Boulder Cave lies along strike and roughly 1,800 m away. According to Palmer (1972), in his study of Onesquathaw Cave, there is a strong tendency for sinking streams to follow cave passages oriented parallel to the strike, in moderately dipping beds. Once Lost Creek reaches the 245 m level, the gradient is reduced and the stream should make its way along strike, emerging at West Boulder Cave.

**Water Chemistry**

*Analysis*

The following chemical data were derived from water samples collected at three sites—Lost Creek Cave, Lost Lakes intake, and West Boulder Cave spring:

| Site | Temp. | pH | $Ca^{++}$ | $Mg^{++}$ | $HCO_3$ (alkalinity) | Hardness |
|---|---|---|---|---|---|---|
| Lost Creek Cave | 9°C | 6.68 | 1.7 ppm | 0.4 ppm | 14.0 ppm | 6.0 ppm |
| Lost Lakes Intake | 16°C | 8.00 | 96.0 ppm | 24.0 ppm | 169.0 ppm | 340.0 ppm |
| West Boulder Cave Spring | 5°C | 7.45 | 4.3 ppm | 1.0 ppm | 31.0 ppm | 15.0 ppm |

Temperature and pH (taken by portable meter) were determined in the field. Water

samples were mailed to the Department of Ecology at Olympia, Washington, for analysis of $Ca^{++}$, $Mg^{++}$, alkalinity, and hardness. Samples were tested within one week. $HCO_3$ is considered as alkalinity (a recent check with portable titration equipment showed little invasion by $CO_2$). The method outlined by Brown (1972, p. 54) was used to determine saturation:

$$(Ca^{++})\ (CO_3^{=}) \qquad K_s$$

$K_s$ from Garrels and Christ (1965)

$$HCO_3 \rightleftharpoons CO_3^{=} + H^+$$

rearranging

$$\frac{(CO_3)\ (H^+)}{HCO_3^-} = K_2$$

$$CO_3^{=} = \frac{(K_2)\ (HCO_3^-)}{H^+}$$

$$K_s = \frac{(Ca^{++})\ (HCO_3^-)\ (K_2)}{H^+}$$

taking negative logs

$$p(K_s) = p(Ca^{++}) + p(HCO_3^-) + p(K_2) - pH^+$$

taking negative logs

$$p(HCO_3^-) + p(K_2) - p(H) = p(CO_3^{=})$$

$p(K)$ from Garrels and Christ (1965)

and $p(CO_3^{=}) + p(Ca^{++}) = p(CaCO_3)$ $\quad pK_s$ from Brown (1972, p. 55)

Therefore:

| Sites | $p(HCO_3^-)$ | + | $p(K_2)$ - $p(H)$ | = | $p(CO_3^{=})$ | + | $p(Ca^{++})$ | = | $p(CaCO_3$ | $p(K_s)$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Lost Creek | 3.854 | + | 10.50 - 6.68 | = | 7.674 | + | 4.770 | = | 12.444 | 8.14 |
| Lost Lakes | 2.772 | + | 10.42 - 8.00 | = | 5.192 | + | 3.018 | = | 8.210 | 8.23 |
| West Boulder Cave | 3.509 | + | 10.56 - 7.45 | = | 6.619 | + | 4.366 | = | 10.985 | 8.09 |

$p(K_s)$ (from Garrels and Christ, Table 3.2) shows the expected K if the water were saturated with respect to $CaCO_3$. Since $p(CaCO_3)$ at Lost Creek Cave and West Boulder Cave is greater than $p(K_s)$ (greater because of the use of negative logs), these two locations are undersaturated with respect to calcite. At Lost Lakes the water is slightly supersaturated with respect to calcite.

### Discussion

All of the chemical data support the conclusion that West Boulder Cave and not Lost Lakes is the outlet for Lost Creek. Water in the sinking stream is undersaturated with respect to calcite. At West Boulder Cave the water is slightly more saturated than in upper Lost Creek. This situation is to be expected as Lost Creek is moving rapidly through the cave so that water would not be in contact with the cave walls long enough to dissolve much carbonate.

On the other hand, the Lost Lake inlet is supersaturated with calcite and contains a much greater amount of dissolved material, suggesting a slow movement of ground

water. While the water may have originated from Lost Creek, it is more likely that this water represents surface seepage into the moraine and limestone below the Lost Creek swallow hole.

### Geomorphic History

The history of the Lost Creek-West Boulder drainage and associated cave system is difficult to interpret and may be revised after more detailed studies are made. The following conclusions seem reasonable:

a. Lost Creek and West Boulder drainages were established prior to glaciation. There may have been some water flowing into what is now the present cave system through small fissures and joints but the bulk of the water was flowing down the old lower Lost Creek valley. The junction of Lost Creek and the West Boulder River was probably near the Burnt Leather Ranch (Fig. 2).
b. Glaciers cut a U-shaped valley in upper Lost Creek and desposited moraine into the lower valley, filling it downstream from Lost Lakes. Glacial retreat formed the moraine-dammed Lost Lakes.
c. Lost Creek cut a channel into the moraine, reaching bedrock at the Lost Creek Cave site. Abundant glacial melt-water from the receding Lost Creek glacier accelerated cave formation, enlarging cave passages until the entire creek was pirated underground, leaving lower Lost Creek as a dry valley.
d. Since the end of glaciation, cave excavation has proceeded at a reduced rate with passage enlargement occurring mainly by corrosion during spring runoff rather than by corrosion from acidic groundwater.
e. Lost Creek Cave is entirely bedding-plane controlled and is not related to nearby Lost Creek fault. The cave is formed in the southwest limb of the Lion Mountain syncline and the underground flow is probably along strike following a single massive carbonate unit in the Madison Group.

Groundwater flow systems that at first glance appear to be relatively simple can prove to be quite complex, especially in areas of high relief and diverse geology. Other underground flow systems in Montana and Wyoming similar to Lost Creek should be examined carefully with this fact in mind.

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# Pollen Analysis of Wildcat Lake, Whitman County, Washington: The Last 1000 Years

## Abstract

Variations in the microfossil and organic content of four meters of sediments, spanning the last 1000 years, reflect changes in both aquatic and terrestrial environments. However, the most significant event represented in the fossil and sedimentary record resulted from the introduction of livestock and subsequent destruction of the natural vegetation, proliferation of weeds, and erosion. These events are marked by increased deposition rates, pollen concentration per $cm^3$, moss and fungal spores, and weed pollen percentages.

Wildcat Lake underwent several substantial changes in depth and volume prior to the introduction of European grazing animals. The most important of these occurred 400-500 B. P., about the time of the fall of Mt. St. Helens W volcanic ash. The event, believed to represent deeper and fresher water, is marked by increased *Ruppia, Pediastrum,* and *Spirogyra.*

## Introduction

In order to obtain information on the Holocene vegetation and climate of southeastern Washington, several cores were obtained from Wildcat Lake, 3 km south of Hooper, Washington. The site was selected because, unlike many small scabland lakes, Wildcat Lake has never completely dried nor has it been "improved" by dredging within the memory of local residents. Preliminary sampling by Washington State University palynology classes and initial examination of the cores by Glen Green revealed well preserved microfossils, rapidly changing sediment types, the presence of Mt. St. Helens W volcanic ash, and an unusually rapid deposition rate. Since all of these characteristics could contribute to a detailed environmental chronology, additional cores were collected by P. Mehringer and K. Petersen with the cooperation of the Washington State University Archaeology Field School.

These additional cores, over 14 m long, ending in Mt. Mazama volcanic ash, also contained Mt. St. Helens Y volcanic ash and provided numerous radiocarbon dates, preliminary analysis experience for palynology classes, and two Master's Theses (Davis, 1975; Kolva, 1975). In this paper we report analysis of the upper four meters of Wildcat Lake sediments that span approximately 1000 years of deposition prior to and including the introduction of grazing animals.

Pioneering palynology in Washington's scablands (Hansen, 1941, 1943, 1944, 1947) was restricted to peat deposits and was characterized by wide sampling intervals, exclusion of "non-indicator" pollen types, and an emphasis on forest succession. Modern

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palynological techniques used at Wildcat Lake include close interval sampling, absolute pollen counts (pollen/$cm^3$ of sediment), and the identification of most pollen types and algae. Similar techniques have led to better understanding of forest succession in other parts of the world, but few comparative studies are available for semi-arid grasslands and deserts.

H. P. Hansen did not emphasize the effects of European culture in pollen diagrams from eastern Washington. Hansen (1941) mentioned possible effects of grazing and cultivation at Crab Lake, but because of disturbance, surface samples were not analyzed. Later work at Harrington and at Wilbur, Washington, illustrated dramatic increases of Gramineae, Chenopodiaceae, and Compositae in surface samples (Hansen, 1944).

#### Pollen Analysis and Agriculture

The introduction of agriculture is an important event reflected in pollen diagrams from sites throughout the world. Pollen diagrams from Denmark (Iversen, 1956) show the effect of primitive agriculture and forest clearance. The pollen of climax forest trees is replaced by pollen of less shade tolerant species and by grass and weed pollen. *Urtica* and *Plantago* pollen become abundant with Roman settlement at 2200 B. P. near Lago di Monterosi, Italy (Bonatti, 1970). Mayan slash and burn agricultural techniques may have produced cyclical changes in pollen frequencies of *Zea, Ambrosia,* cheno-ams (Chenopodiaceae-*Amaranthus*), and *Solanum* in Guatemala and El Salvador (Tsukada and Deevey, 1967).

Increased erosion and run-off associated with mining and European settlement may have increased the number of fungal spores deposited in Shagawa Lake in northeast Minnesota (Bradbury and Waddington, 1973). In the eastern United States, an increase in *Ambrosia* and cheno-am pollen marks forest clearance and the beginning of farming (Davis, 1967; Webb, 1973). European culture has significantly altered the vegetation and pollen rain of southern Michigan too, but pollen frequencies still reflect major vegetation patterns (Webb, 1973). Alder pollen values increase following forest clearance in coastal Washington (Davis, 1973) and southern British Columbia (Mathewes, 1973).

#### Grazing History of Southeastern Washington

Large herbivores were an important food source for native peoples of southeastern Washington. The bones of wapiti *(Cervus canadensis),* deer *(Odocoileus* spp*),* pronghorn *(Antilocarpa americana),* and mountain sheep *(Ovis canadensis)* are common in archaeological sites spanning the last 10,000 years (Gustafson, 1972). While there are few historic accounts of buffalo in eastern Washington (Schroedl, 1973), bison were hunted along the lower Snake River 2500 to 1500 years ago. From 1500 to 500 years ago, they were more common along the Upper Columbia River. After 500 years ago, Plateau bison populations diminished considerably. Although Plateau peoples never became economically dependent on bison, buffalo hunting became an established cultural pattern (Schroedl, 1973).

Native Americans of eastern Washington acquired horses after A. D. 1730 (Haines, 1938). Daubenmire (1970) suggests that intensive grazing by aboriginal horse herds was restricted to the immediate vicinity of villages, and we assume that the overall effect of Indian horses on steppe vegetation was less than that of subsequent European horse herds.

The first reported cattle in eastern Washington were 632 head driven from San Francisco to the Whitman Mission in 1836 (Cotton, 1904). The Whitman Massacre and

ensuing Indian wars of 1845-55 kept the number of cattle small until 1860 when large-scale cattle ranching began (Boyce, 1937; Snowden, 1909). Walla Walla ranchers pastured their herds in southeastern Washington and drove them to lucrative markets at the Caribou mines in British Columbia. The range had begun to deteriorate by 1869 (Splawn, 1917; Lewis, 1926). From 1873 to 1881, the ranges were severely overstocked because the Canadian and Montana markets had closed (Boyce, 1937).

Farmers began to file claims for previously free cattle range in 1859, and by 1877 settlers were arriving in considerable numbers (Zimmerman, 1915). Wheat was rarely grown by early settlers because high freight rates were charged by steamship lines (Lindsey, 1926). However, when the railroad reached Colfax, Washington, in 1882, wheat acreage doubled (Zimmerman, 1915). Grazing land became wheat fields, and cattle were crowded onto already overstocked rangeland. Livestock ranching remained important in the scablands, where shallow soil prevented cultivation (McGregor, 1974a).

Severe winters in 1880 and 1890 reduced the number of Palouse range cattle and eased grazing pressure. Fifty percent of the range cattle in eastern Washington died in the winter of 1880-81 (Cotton, 1904). The hard winter of 1889-90 nearly ended the range cattle industry (Lewis, 1926; Boyce, 1937).

After horses were no longer needed for cattle ranching, they were allowed to run free and multiply. Between 1890 and 1900, the number of horses in Adams, Franklin, and Whitman Counties nearly tripled (Fig. 1). Although they may have become as destructive to the range as sheep, most of them were shipped to Canada and Africa by 1904, thereby relieving grazing pressure (Cotton, 1904).

Sheep arrived in about 1871, and by 1878 there were 30,000 head in Whitman County (Zimmerman, 1916). Although eastern Whitman County was cultivated, western Whitman County remained sheep country (Lindsey, 1926).

From 1880 to 1890, sheep were the most important element of the Whitman County livestock industry (Lindsey, 1926). The area surrounding Wildcat Lake was regarded as free range until 1895 when the Northern Pacific Railroad brought an injunction against area sheepmen (*Lewiston Morning Tribune*, Feb. 19, 1974). The McGregors rented and later bought railroad lands surrounding Wildcat Lake (Lindsey, 1926). They wintered their sheep in the scablands, often staying in small sheepherder's cabins (McGregor, 1974a). From 1905 to 1920, Wildcat Lake basin was a lambing camp. During the winter months, flocks of about 2000 ewes were driven to Wildcat Lake. After giving birth, the flock rejoined the main herd and was replaced by another flock (McGregor, 1974b).

Figure 1, based on U.S. Census figures from 1864 to 1972, shows the number of grazing animals in Adams, Franklin, and Whitman Counties, Washington, since 1860. The figure does not include animals sold (transported elsewhere) during the census year, so the grazing pressure may have been greater than indicated. The figure includes animals fed in farm pastures and on native grassland.

The number of censused cattle increased suddenly between 1870 and 1890, and remained constant until 1930 when it again increased. After 1890, range cattle were replaced by dairy cattle and registered cattle (Boyce, 1937). By 1940, automated farm machinery and the automobile had nearly replaced horses. The number of sheep increased steadily until 1935, but they were thereafter replaced in importance by cattle. Price ceilings on wool and higher labor costs after World War II made sheep raising less profitable than cattle ranching. While the McGregors remained sheepmen, many sheep ranches became cattle ranches (William McGregor, verbal communication).

**Study Area**

Wildcat Lake (Elev. 335 m, NW ¼ SE ¼, sec. 3, T. 14N., R. 37 E., Starbuck Quad., Washington) is located 3 km south of Hooper, Washington, in the channeled scablands (Figs. 2 and 3). The scablands are zones of isolated loess islands surrounded by interlocking

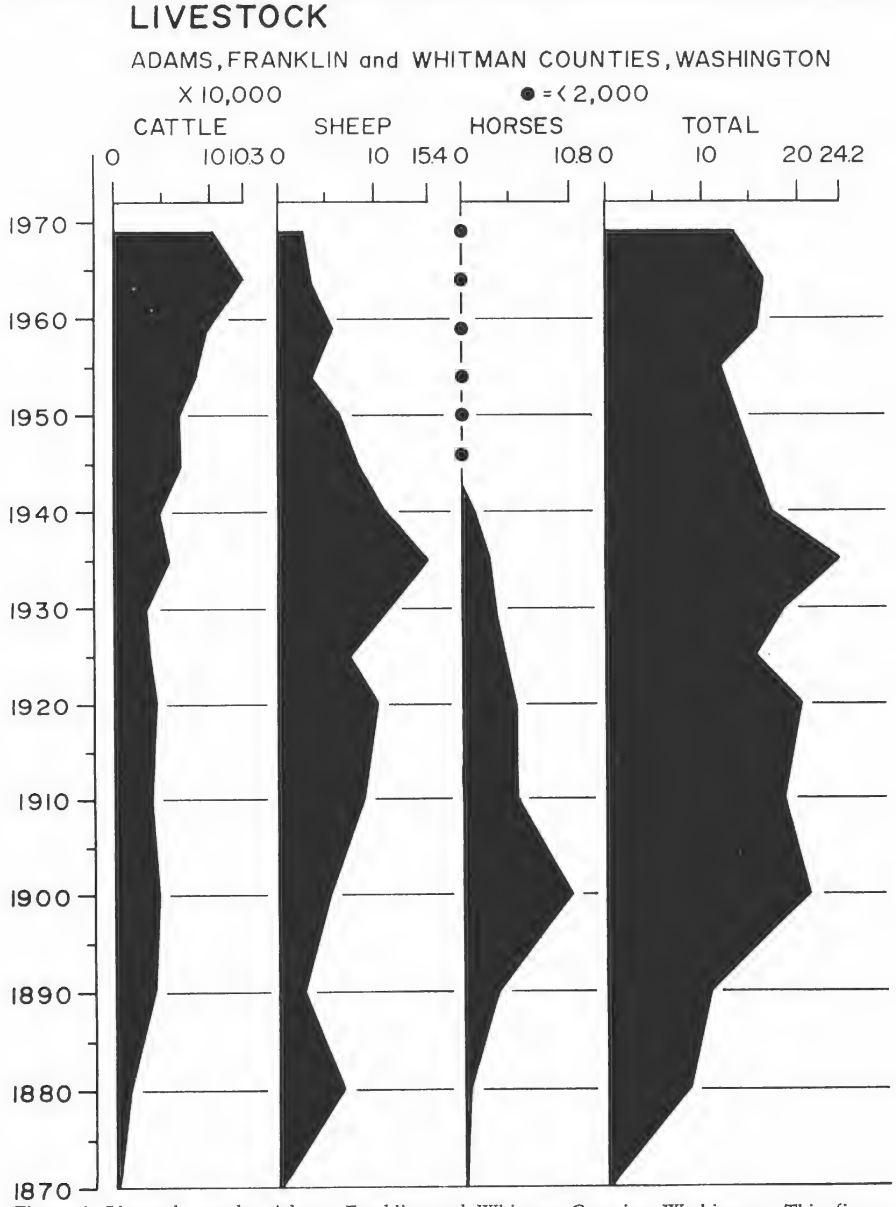


Figure 1. Livestock trends: Adams, Franklin, and Whitman Counties, Washington. This figure shows the number of livestock during census years based on U.S. Census (1864-1972) data.

channels of exposed Miocene basalt. This formerly loess-covered landscape was stripped by the late Quaternary castastrophic flooding of Glacial Lake Missoula (Baker 1973; Bretz, 1923, 1959, 1969; Bretz *et al.*, 1956; Richmond *et al.*, 1965). The deluge violated the Palouse-Snake River divide, scouring numerous cataracts and rock basins by joint controlled channeling (Trimble, 1905). The small (1-3 ha), shallow (1-3 m)

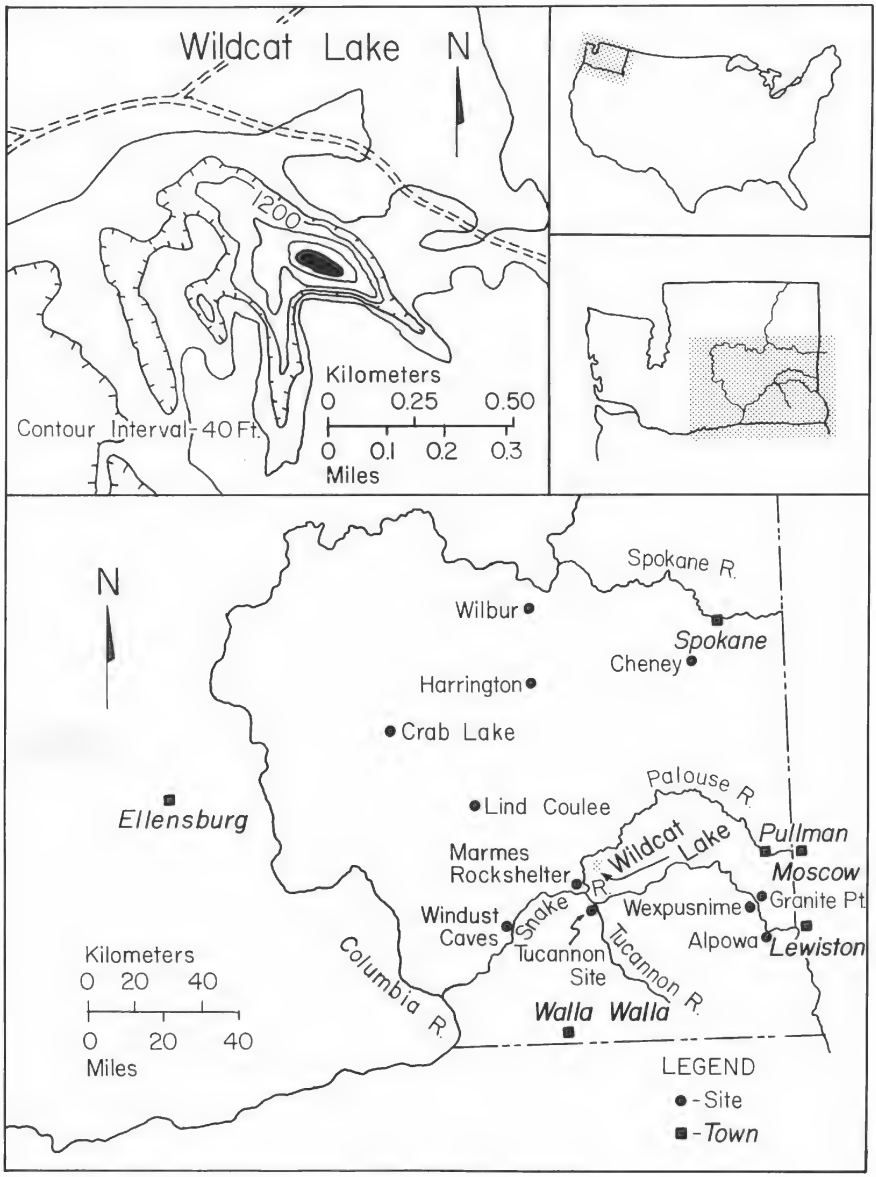


Figure 2. Wildcat Lake locality.

Figure 3. Wildcat Lake, view to the east. The photograph was taken in May, 1974 during an abnormally moist spring. (Photo by D. Kolva)

lake lies in one of these vertical rock-walled coulees (Wolcott, 1964), which Bretz *et al.* (1956) described as a great empty hole more than 120 ft deep. There is no sedimentary evidence that it has dried nor has it completely dried in the memory of local residents. A water sample taken on October 27, 1974, showed Wildcat Lake to be basic (pH 9.0), alkaline, and saline (Davis, 1975).

Precipitation in southeastern Washington is low during the six warmest months (May-October), with two-thirds of the annual precipitation (16.66 in at Walla Walla, Washington) falling from November to April. While southwesterly winds predominate, north and east winds are common in the spring (April and May) and late autumn (September and October) (Phillips, 1970). Effective precipitation has risen since drought in the early 1930's (Davis, 1975), but Fowler and Helvey (1974) found that the effect of irrigation on temperature and precipitation in southeastern Washington was minimal.

Wildcat Lake lies in the north central section of the *Agropyron-Festuca* vegetation zone in southeast Washington (Daubenmire, 1970). *Agropyron spicatum* (nomenclature follows Hitchcock and Cronquist, 1973) and *Festuca idahoensis* are dominant on zonal soils, but deep soils are rare in the flood-swept scablands, and lithosolic associations occupy most of the landscape.

The *Agropyron-Festuca* zone is bounded on the west by the slightly warmer and drier *Artemisia tridentata-Agropyron spicatum* zone and the cooler and drier *Artemisia tridentata-Festuca idahoensis* zone. To the north lies the cooler *Artemisia tripartita-Festuca idahoensis* zone and to the east the cooler and more moist *Festuca-Symphoricarpos* and *Festuca-Rosa* zones (Daubenmire, 1970).

Most species affected by intensive grazing (Daubenmire, 1939, 1940; Moomaw, 1956) are not heavy pollen producers. However, grasses and members of the Compositae, which often produce air-borne pollen, are affected. Three grasses *(Agropyron spicatum, Festuca idahoensis,* and *Bromus tectorum)* decrease in frequency with heavy grazing by sheep, but the coverage of *Poa sandbergii* increases. Three species of Compositae *(Agoseris heterophylla, Achillea millefolium lanulosa,* and *Lagophylla ramosissima)* decrease, while four *(Agoseris glauca, Stephanomeria paniculata, Antennaria dimorpha,* and *Erigeron pumilus intermedius)* increase with heavy grazing. *Madia exigua* increases markedly in frequency with intermediate grazing (Daubenmire, 1940).

Fire affects the vegetation of different zones in different ways. For example, *Artemisia tridentata* is easily killed by fire; therefore, the effects of fire are more long-lasting in vegetation dominated by *A. tridentata* than in vegetation dominated by grasses. The effects of burning are also different between native and disturbed stands. Daubenmire (1975) reports that fire temporarily favors *Poa sandbergii* in a native stand of the *Festuca idahoensis-Poa sandbergii* association, but the effects are short-lived, and the balance is restored in twelve years. In an adjacent abandoned field, which is dominated by *Bromus tectorum,* the results of fire are again temporary, but the disclimax is maintained (*i.e., Bromus tectorum* retains dominance).

As available moisture increases, steppe vegetation intergrades into ponderosa pine *(Pinus ponderosa)* forest followed, with increasing elevation, by Douglas-fir *(Pseudotsuga menziesii),* lodgepole pine *(Pinus contorta),* grand fir *(Abies grandis),* western white pine *(Pinus monticola),* Engelmann spruce *(Picea engelmannii),* and subalpine fir *(Abies lasiocarpa).* Hemlock *(Tsuga heterophylla* and high altitude *T. mertensiana)* occur in the Cascade mountains 140 km to the west. Pine forest lies 40 km southeast of Wildcat Lake in the Blue Mountains and 55 km to the east near Colfax, Washington.

Cupressaceae: western red cedar *(Thuja plicata),* yellow cedar *(Chamaecyparis nootkatensis),* dwarf juniper *(Juniperus communis),* western juniper *(J. occidentalis),* and Rocky Mountain juniper *(J. scopulorum)* are found on the eastern slopes of the Cascades. Red cedar grows in northeastern Washington and northern Idaho, within 80 km of Wildcat Lake.

Garry oak *(Quercus garryana)* grows in xeric areas 160 km southwest of Wildcat Lake (Taylor and Boss, 1975). Hackberry (*Celtis* sp.) is found within the *Agropyron-Poa* zone on colluvial aprons along the Snake River and a short distance up the Palouse River (Daubenmire, 1970). Alder (*Alnus* sp.) typically abuts hackberry at the lower end of narrow canyons where it grows along stream courses (Daubenmire, 1970). Willows (*Salix* sp.) are widespread along most streams in Washington. The closest willows grow along the Palouse River at Hooper, 3 km north of Wildcat Lake and at Wind Lake, 6 km to the south. Birches *(Betula occidentalis)* are also found along most streams in the steppe and ponderosa pine forests in eastern Washington. Hazel (*Corylus* sp.) is a major understory dominant in Oregon's Willamette Valley 300 km southwest of Wildcat Lake (Franklin and Dyrness, 1973).

The landscape surrounding Wildcat Lake is dotted with small depressions created by the scabland flood. These shallow basins of closed drainage ordinarily support stands of *Distichlis stricta,* but they contained standing water surrounded by sedges in the unusually moist spring of 1974. By October, the water holes had dried and were supporting stands of *Distichlis.*

Aquatic vegetation at Wildcat Lake includes sedges, *Phragmites communis,* and *Ruppia maritima.* A single dwarfed nonreproducing *Typha* plant was found in the spring of 1974. Algae (*Cladophora* sp. and *Ulothrix* sp.) were growing on *Ruppia* in shallow water, and a *Cladophora* mat covered much of the lake surface in the fall of 1974.

*Ruppia maritima,* abundant in shallow lakes of the Columbia Basin (Yocom, 1951), is found typically in shallow, brackish water. However, Mayer (1967) found that under disease-free conditions, and without competition, *Ruppia maritima* grows and reproduces best in fresh water. An unidentified infection retarded growth of *Ruppia* seedlings, particularly in salt concentrations below 3000 ppm, but when an algicide-fungicide was added, maximum growth took place in fresh water.

#### The Core

The Wildcat Lake core consists primarily of soft, granular, non-laminated, slightly elastic, slightly plastic, slightly sticky, algal gyttja of variable color and texture. Exceptions to these characteristics are noted in the core description (Table 1). The sediments contain insect parts, *Ruppia* seeds, layers of ash-rich loess, and Mt. St. Helens W volcanic ash. Large (100 micrometers) charcoal fragments are abundant throughout the core. The entire core contains carbonates (determined by effervescence in 10 percent HCl).

The color values given are from the Munsel Color Chart. The description of bands (layers differing primarily in color from adjacent sediments) and laminations (layers differing primarily in texture and/or adhering poorly to adjacent sediments) follows Soil Survey Manual (1951) terminology for platy structure. Abundance categories of *Ruppia* seeds follow Johnson *et al.* (1960) categories for very fine soil pores. Lower boundary distinctness and topography follows Soil Survey Manual (1951) terminology with the following modifications: very abrupt (va) $= <$ 1 mm, abrupt (a) $=$ 1-2 mm, clear (c) $=$ 2-4 mm, gradual (g) $=$ 4-8 mm, diffuse (d) $=$ 8-16 mm. Sediments termed gelatinous bounced when dropped on a table top.

#### Methods

The core sections were taken on August 1-2 and October 1, 1972, with a 10 cm diameter modified Livingston piston sampler (Cushing and Wright, 1965). Plastic core barrels containing the sediments were sawed open, and 8 $cm^3$ (cubes 2 cm on a side) samples were taken at 3 cm intervals from 0.02 m to 0.50 m, at 5 cm intervals from 0.55 to 1.75 m, and at 10 cm intervals from 1.80 to 4.00 m with a device designed by Kolva (1975). Four tablets, each containing 12,500 $\pm$ 500 *Lycopodium* spores used as tracers (Stockmarr, 1971), were added to each sample in dilute HCl before extraction. Extraction followed Mehringer (1967) and included acetolysis; the residue was mounted in silicone oil (2000 centistokes). A minimum of 200 terrestrial pollen grains and 50 introduced *Lycopodium* spores were counted under 400X magnification.

Weight-loss-on-ignition studies were initiated to determine percentage changes in both organic matter and carbonates throughout the core. Eight $cm^3$ samples were dried for 18 hours at 105° C, cooled in a desiccator, and weighed on a Mettler balance. Test samples, dried for 16, 21, 39, and 64 hours, showed no appreciable weight loss after 16 hours. After 4 hours in a 500° C furnace, the samples were cooled and weighed. Carbonates were removed by burning at 950° C for 4 hours. Konrad *et al.* (1970) found that complete oxidation of organic matter and carbonates occurred after burning samples

Table 1. Core Description, Wildcat Lake, Whitman County, Washington

| Depth (Meters) | Description |
|---|---|
| 0.00-0.15 | Clayey gyttja; very dark gray (5Y 3/1); non-elastic, sticky, firm; as. |
| 0.15-0.25 | Sandy silt; dark olive gray (5Y 3/2); non-elastic, firm; as. |
| 0.25-0.37 | Clayey gyttja; black (10YR 2/1); non-elastic, sticky, firm; as. |
| 0.37-0.40 | Sandy silt; very dark gray (10YR 3/1); non-elastic, firm; as. |
| 0.40-0.47 | Clayey gyttja; black (10YR 2/1); non-elastic, sticky, firm; as. |
| 0.47-0.51 | Gyttja; dark reddish brown (5YR 3/2); vas. |
| 0.51-0.59 | Gellatinous gyttja; dark reddish brown (5YR 3/4); strong, very thin laminations; very elastic; few insect fragments and *Ruppia* seeds; as. |
| 0.59-0.70 | Silty gyttja; very dark gray brown (10YR 3/2); non-elastic, very plastic; few *Ruppia* seeds; gs. |
| 0.70-0.77 | Silty gyttja; black (10YR 2/1); plastic, very sticky; few *Ruppia* seeds; ds. |
| 0.77-0.85 | Gyttja; dark brown (10YR 3/3); very plastic; many *Ruppia* seeds; as. |
| 0.58-0.89 | Gyttja; dark yellowish brown (10YR 4/5); weak, thin laminations; elastic, plastic, non-sticky, firm; very few *Ruppia* seeds; aw. |
| 0.89-0.94 | Silty gyttja; dark brown (10YR 3/3); few *Ruppia* seeds; as. |
| 0.94-1.47 | Silty clay gyttja; dark olive (5Y 3/4); many *Ruppia* seeds from 0.99 to 1.02 m, otherwise few; cs. Radiocarbon sample taken from 1.05 to 1.15 m. |
| 1.47-1.55 | Silty clay gyttja; dark brown (7.5YR 3/2); non-elastic, non-plastic; few *Ruppia* seeds; vas. |
| 1.55-1.57 | Mt. St. Helens W volcanic ash; white (5Y 8/2); many *Ruppia* seeds; vas. |
| 1.57-1.85 | Gyttja; very dark gray brown (10YR 3/2); non-plastic, very sticky; ds. Radiocarbon sample taken from 1.58 to 1.68 m. |
| 1.85-1.87 | Gelatinous gyttja; dark red (2.5YR 3/6); elastic, very sticky; vas. |
| 1.87-2.35 | Gyttja; very dark gray brown (10YR 3/2); very sticky; *Ruppia* seeds common from 1.90 to 1.94 m; ash-rich loess layer at 2.03 m; ds. |
| 2.35-2.40 | Gyttja; very dark gray (10YR 3/1); grs. |
| 2.40-2.54 | Gyttja; very dark gray brown (10YR 3/2); very sticky; *Ruppia* seeds common from 2.47 to 2.50 m; ds. |
| 2.54-2.60 | Gelatinous gyttja; dark reddish brown (2.5YR 3/4); very elastic; as. |
| 2.60-2.70 | Gelatinous gyttja; very dark gray brown (10YR 3/2); very elastic; cs. |
| 2.70-2.77 | Gelatinous gyttja; dusky red (2.5YR 3/2); very elastic, firm; cs. |
| 2.77-2.94 | Clayey gyttja; dark reddish brown (5YR 2/2); plastic, very sticky; very few *Ruppia* seeds; vaw. |
| 2.94-3.01 | Gelatinous gyttja; olive brown (2.5Y 3/4); very elastic, firm; vaw. |
| 3.01-3.25 | Clayey gyttja; black (5YR 2/1); very sticky, firm; ds. |
| 3.25-3.43 | Gelatinous gyttja; very dark gray brown (10YR 3/3) to olive brown (2.5Y 3/4); very elastic; cs. Radiocarbon sample taken from 3.21 to 3.29 m. |
| 3.43-3.54 | Gyttja; dark reddish brown (5YR 3/2); very sticky; few *Ruppia* seeds; cs. |
| 3.54-3.86 | Gelatinous gyttja; dark brown (7.5YR 3/2) to olive brown (2.5Y 3/4); very elastic; few *Ruppia* seeds from 3.63 to 3.83 m; as. |
| 3.86-3.98 | Gyttja; very dark brown (10YR 2/2); very sticky; as. Radiocarbon sample taken from 3.80 to 3.90 m. |
| 3.98-4.00 | Gelatinous gyttja; olive brown (2.5Y 3/4); very elastic, firm; vas. |

for 20 minutes at 650° C and 950° C, respectively. Percent organic-matter and percent carbonate weight-losses were calculated as percent of the dry weight.

The pollen diagram (Fig. 4) is divided into six sections: the number of pollen grains per $cm^3$, terrestrial pollen, aquatic pollen, total pollen, algae, and weight-loss-on-ignition. Aquatic pollen and algae are excluded from the pollen sum and are presented as percent of total pollen. Because of very high percentages, the *Botryococcus* scale is smaller than scales to the left. Some tree pollen curves have been combined because of low percentages. These include *Abies* + *Picea* + *Tsuga* + *Pseudotsuga* and *Betula* + *Corylus*.

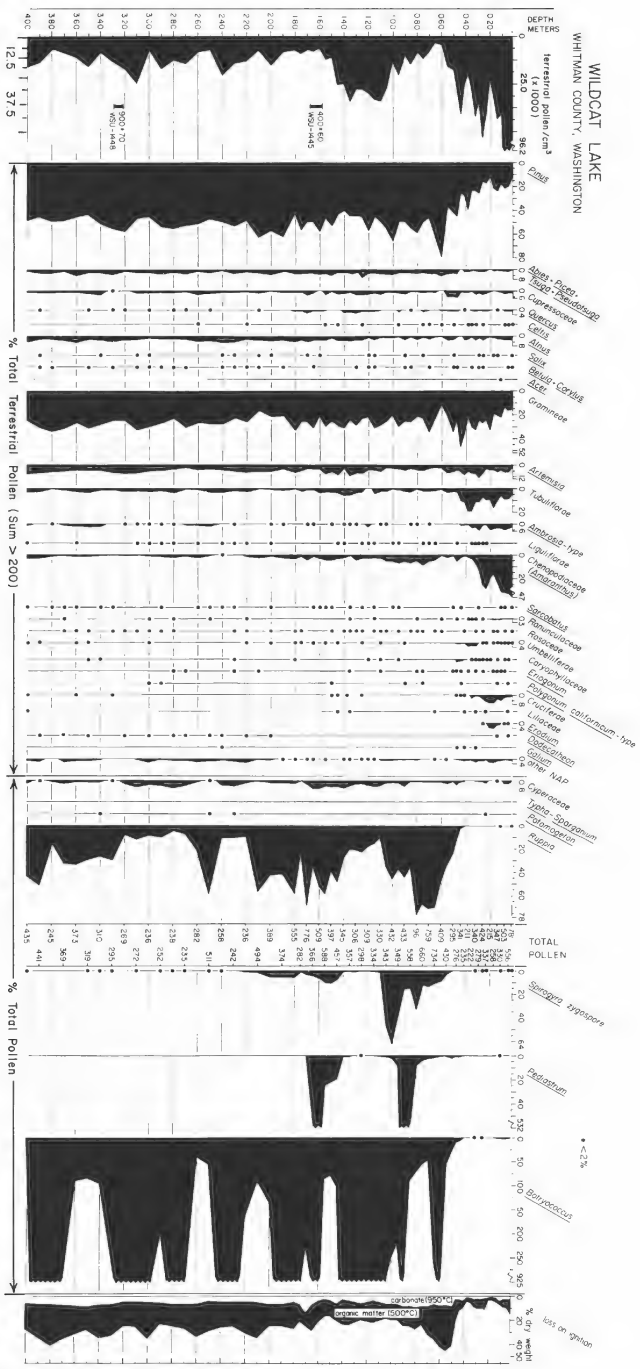


Figure 4. Wildcat Lake pollen diagram.

"Other NAP" includes single occurrences, undeterminable pollen, and unidentified pollen. Dots represent less than 2 percent. The number of pollen grains per $cm^3$ is calculated as:

$$\text{Number of Grains/cm}^3 = \frac{\text{Native Grains Counted}}{\text{Tracers Counted}} \times \frac{\text{Tracers Added}}{\text{cm}^3 \text{ of Sediment}}$$

**Results and Discussion**

With few exceptions the terrestrial pollen record from 4.00 to 0.47 m appears stable. *Pinus* varies around 50 percent with peaks at 2.10 m ( 63 percent), 1.90 m (62 percent), and 0.60 m (80 percent). Gramineae, comprising about 30 percent of terrestrial pollen, mirrors *Pinus* throughout most of the section. Arboreal pollen types, excluding pine, are less than 10 percent throughout the core. *Abies* + *Picea* + *Tsuga* + *Pseudotsuga* varies from 1 percent to 8 percent and Cupressaceae reaches 6 percent at 0.50 m. *Quercus* does not rise above 4 percent and *Betula* + *Corylus, Celtis,* and *Acer* never attain 2 percent. *Alnus* varies between 2 percent and 7 percent throughout the diagram.

Below 0.47 m individual non-arboreal pollen types, excepting Gramineae, are never higher than 10 percent. *Artemisia* reaches 9 percent at 1.35 m, but *Ambrosia*-type pollen never exceeds 6 percent, and Liguliforae remains less than 2 percent. Cheno-ams vacillate around 1 percent from 3.80 to 2.20 m and around 3 percent from 2.20 to 1.80 m.

In contrast, *Pinus* percentages drop to 20 percent above 0.47 m as non-arboreal pollen percentages increase. Cruciferae, *Ambrosia*-type and cheno-am pollen percentages increase above 0.40 m and Tubuliflorae frequency increases above 0.50 m. Cheno-am values decrease at 0.17 m where Tubuliflorae, Cruciferae, and *Erodium* pollen percentages increase.

While the terrestrial pollen record is fairly stable from 4.00 to 0.47 m, dramatic changes occur in aquatic pollen and algae percentages. *Spirogyra* zygospores, rare below 2.00 m, reach high values at 1.60 m and from 1.10 to 0.60 m corresponding to high *Ruppia* and *Pediastrum* percentages. *Pediastrum* first becomes abundant at 1.70 m and high percentages at 1.60 and 0.90 m precede low *Botryococcus* values at 1.50 and 0.70 m. *Botryococcus* percentages reach 925 percent of total pollen at 3.90 m and are high from 1.40 to 1.00 m where *Pediastrum, Spirogyra,* and *Ruppia* values are low.

Identification of *Spirogyra* zygospores is based on similarities in size and morphology to illustrations by Rabenhorst (1937), Transeau (1951), and Randhawa (1959). Most of these microfossils (probably the middle chitinous layer of the three-layered zygospore wall) were smooth, but occasional wrinkled types (Fig. 5) were observed. *Spirogyra* is most abundant in freshwater lakes at the Grand Coulee (Castenholz, 1957).

*Botryococcus braunii* is a cosmopolitan species more salt tolerant than *Pediastrum boryanum.* It occurs in both fresh and saline waters in the Grand Coulee (Castenholz, 1957) and North Dakota (Moore and Carter, 1923). *Botryococcus* was found in waters less saline than 9400 ppm total dissolved solids in the Grand Coulee. It was more abundant in saline Alcove and Lenore lakes in the fall of 1955 and 1956.

*Pediastrum boryanum* is abundant in freshwater Alkali Lake in the Grand Coulee, and does not occur in waters more saline than 4000 ppm total dissolved solids (Castenholz, 1957). Fossil occurence of *P. boryanum* has been correlated with cold, oligotrophic waters at Lago di Monterosi, Italy (Goulden, 1970). *P. boryanum* frequency is greater in sediments deposited under oligotrophic conditions at Potato Lake, Arizona (White-

side, 1965), and it disappears with the development of peatland at Myrtle Lake in northern Minnesota (Janssen, 1968). Rawson (1956) considers *P. boryanum* an indi-

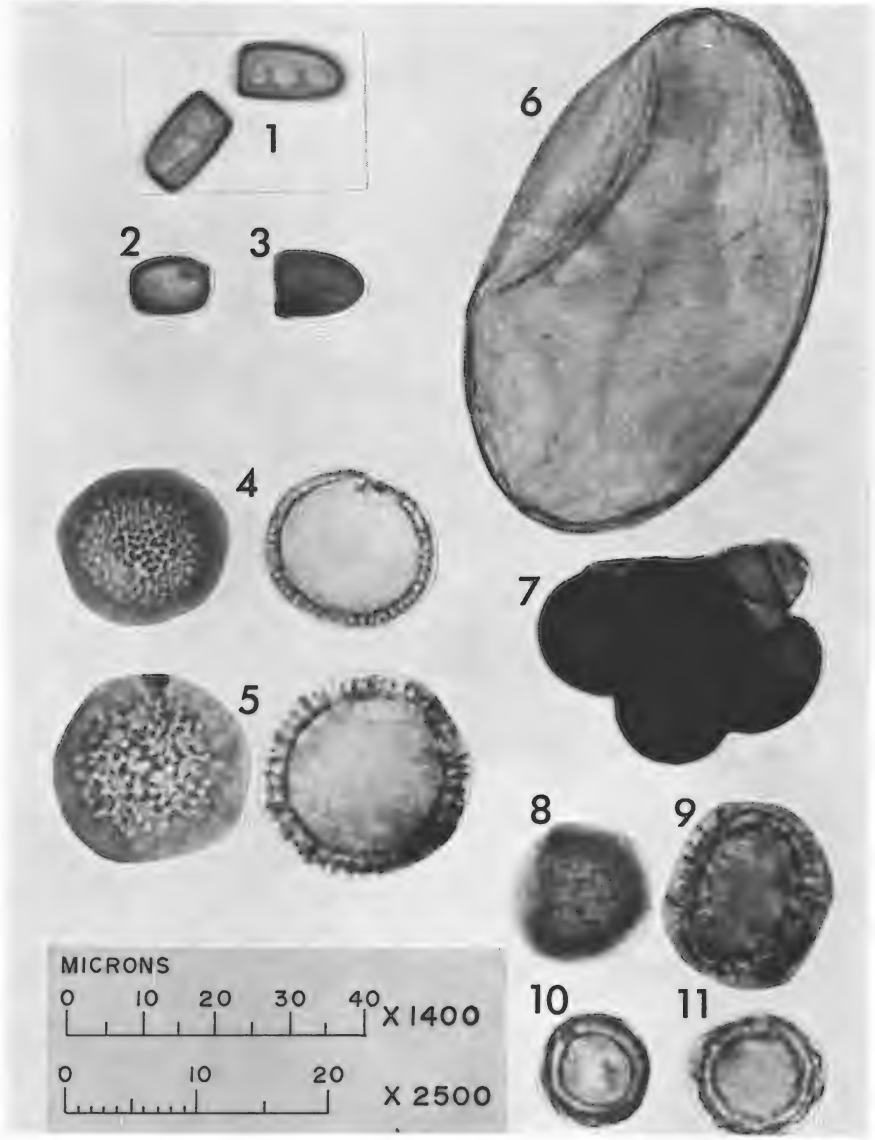


Figure 5. Selected spore types. 1. *Sporomiella minima* reference slide, courtesy of Dr. J. Rogers (X 2500). 2. *Sporomiella* fossil, 0.35 m Wildcat Lake (X 1400). 3. *Sporomiella* fossil, 0.41 m Wildcat Lake (X 1400). 4. Moss spore fossil, 0.41 m Wildcat Lake (X 2500). 5. *Tortula ruralis* reference specimen, Univ. Utah Herbarium No. 3327 (X 2500). 6. *Spirogyra* zygospore fossil, 0.80 m Wildcat Lake (X 1400). 7. Type 4 fossil, 0.80 m Wildcat Lake (X 1400). 8 and 9. Type 8 fossil, 0.20 m Wildcat Lake (X 2500). 10. Type 12 fossil, 0.35 m Wildcat Lake (X 2500). 11. Type 12 fossil, 0.14 m Wildcat Lake (X 2500).

cator of mesotrophic (intermediate to oligotrophic and eutrophic) waters, but actual physiological tolerances of the species vary (Castenholz, 1957). Also, there may be distinct physiological races that show little morphological differentiation (Rawson, 1956).

Photographs were taken of each spore-type encountered and their numbers recorded at each depth. Moss spores and fungal spores resembling coprophilous and plant-pathogenic types were found in Wildcat Lake sediments. *Sporormiella* spores are most abundant at 0.35 and 0.17 m and are rare below 0.50 m (Davis, 1975). *Sporormiella* spores are composed of four or more dark brown to blackish, transversely-septate cells with a germ slit in each cell. Fruiting bodies (ascostromata) of this fungus are common on the dung of herbivorous animals (Munk, 1957). Morphologic characteristics of *Sporormiella* are apparent in the fossil spores and in spores from the reference slide in Figure 5.

Spore type 12, a small (8 micrometer) spore with a single pore (Fig. 5) is the most abundant spore type from 0.20 to 0.14 m. It may be a grass pathogen such as *Plasmospora, Phytophthora, Pythium, Ustilago,* or *Tilletia.* Spore type 8 (Fig. 5), abundant at 0.14 m, may also be a grass pathogen such as *Ustilago.* Type 4 (Fig. 5) may be a plant pathogen such as *Urocystis* or it may be bulbules of a dematiaceous hyphomycete, but no confident identification was made. It is the most abundant spore type below 0.50 m.

Small (10 micrometer) moss spores (Fig. 5) with baculate sculpturing, resembling *Tortula ruralis* spores (Fig. 5), are abundant from 0.47 to 0.26 m and are present in smaller numbers thereafter. Drs. J. D. Rogers and R. Duran (verbal communication) noted similarities between this spore type and the spores of some rusts. Daubenmire (1940) found the frequency of mosses in the *Agropyron-Festuca* association scarcely affected by grazing.

Percent organic-matter weight-loss averages about 29 percent from 4.00 to 1.60 m dropping to an average of 21 percent from 1.55 to 0.75 m. A period of high average weight-loss (39 percent) from 0.70 to 0.50 m is followed by low weight-loss (9 percent) from 0.47 to 0.02 m. Carbonate weight-loss remains low throughout the core; the highest value (14 percent) occurs at 1.70 m.

Below 0.47 m there is an apparent negative correlation between organic-matter loss and the number of pollen grains per $cm^3$. High weight-loss from 0.70 to 0.50 m coincides with low numbers of pollen grains per $cm^3$. Between 1.55 and 0.75 m and from 0.47 to 0.02 m low weight-loss percentages correspond to high numbers of pollen grains per $cm^3$. Above 0.47 m the percent organic-matter loss is much lower, and the relationship of pollen per $cm^3$ to organic-matter weight-loss is reversed at 0.38 m and from 0.20 to 0.17 m where lower weight-loss coincides with decreased numbers of pollen per $cm^3$.

#### Conclusions

Intensive grazing produced changes unprecedented in pollen deposition at Wildcat Lake for the previous 2000 years (Kolva, 1975). Range deterioration allowed the proliferation of weeds while grazing-induced erosion increased the deposition rate, and contributed to the disappearance of aquatic plants and algae. An inferred climatic event immediately following the deposition of Mt. St. Helens W volcanic ash about 450 years ago (Crandell and Mullineaux, 1973) changed the lake depth and water chemistry, but had little effect on the frequency of terrestrial pollen.

Confident evaluation of pre-grazing aquatic environments of Wildcat Lake is diffi-

cult, and several conflicting interpretations are possible. The following interpretations are offered, but analysis of other sites in southeastern Washington is necessary before prehistoric climate and vegetation can be understood.

Although Mt. St. Helens W volcanic ash (1.55 m) may have affected lake chemistry, we believe that high algal and aquatic pollen percentages, the consistently high number of grains per $cm^3$, and the uniformly low organic weight-loss percentage from 1.55 to 0.70 m are the products of a period of greater lake depth and/or decreased productivity and salinity. Since high *Pediastrum* percentages at 1.60 and 0.90 m correspond closely with high *Spirogyra* and *Ruppia* values, similar conditions probably prevailed during the two periods of sediment deposition. The intervening lower values may indicate a return to saline, more productive conditions or they may indicate increased lake depth and mineral dilution.

The high *Botryococcus* percentages from 1.40 to 1.00 m tend to support the first alternative since *Botryococcus* is more abundant in saline than freshwater lakes in the Grand Coulee (Castenholz, 1957). However, the second alternative seems more likely. We believe that as the lake level rose, conditions favoring mesotrophic *Pediastrum* were met, and the lake became sufficiently dilute for *Spirogyra* and *Ruppia* to flourish. As lake level continued to rise, the water became too dilute for *Pediastrum,* and too deep (and/or dilute) for *Spirogyra* and *Ruppia. Ruppia* may have become victim to diseases associated with a freshwater environment (Mayer, 1967). Higher Cyperaceae values from 1.70 to 0.90 m (and from 3.20 to 2.70 m) may result from increased lake perimeter (*i.e.,* increased habitat) or to an increase in the number of sedge-ringed pools in the surrounding scablands.

Increased lake depth would lead to decreased salinity and, conceivably, to decreased productivity (Whittaker and Fairbanks, 1968). Decreased productivity could have produced the slightly lower organic-matter weight-loss from 1.55 to 0.75 m (Fig. 4), and a slower deposition rate reflected in the greater number of pollen grains per $cm^3$. This change in deposition rate between dated events prevents the calculation of absolute pollen influx.

Since Wildcat Lake occupies a basin of closed drainage, it seems likely that greater lake depth was produced by greater effective precipitation. The lack of major changes in terrestrial pollen frequencies prior to the introduction of grazing indicates stability of the vegetation contributing pollen to Wildcat Lake. Later, as the lake became more shallow and/or more mesotrophic, conditions again favored *Spirogyra, Ruppia,* and *Pediastrum* (high values from 1.00 to 0.60 m).

There are several possible interpretations for the lower number of pollen grains per $cm^3$, the high organic-matter weight-loss and high pine percentages in samples from between 0.70 and 0.50 m. Possibly they represent a continuation of the trend toward lower lake level. As the lake level continued to drop, sediment accumulation and low effective precipitation may have produced a very shallow productive lake unfavorable to *Spirogyra* and *Pediastrum.* Increased productivity could have resulted in increased organic deposition, which, in turn, increased the organic percentage of the sediments and decreased the number of grains per $cm^3$ in each sample.

Although pine pollen percentages are high at 0.60 m (Fig. 4), the number of pine grains per $cm^3$ is not (Davis, 1975); therefore, the high pine percentages are an artifact of a low pollen sum. If decreased lake depth is the product of decreased effective

precipitation, the increased pine percentages may be due to drought and decreased pollen production by local plants (Mehringer, Martin, and Haynes, 1967).

Alternatively, the low pollen concentration and high organic content from 0.70 to 0.50 m could result from decreased deposition of silt and pollen. Therefore, the high organic percentage may be an artifact of decreased inorganic deposition at a time when less silt and fewer pollen grains from local plants were reaching the lake. Again, high pine percentages would result from continued long-distance transport of pine pollen. Also, since the clear effects of human disturbance follow close behind, these variations may, somehow, represent earliest disturbance.

The disappearance of *Ruppia, Pediastrum,* and *Botryococcus* microfossils at 0.47 m may reflect a major change in water chemistry associated with sheep, horses, and cattle watering from Wildcat Lake. Increased slope-wash increased the inorganic content of the sediments and accelerated the deposition rate. But, at the same time, increased pollen production by weedy species contributed to a threefold increase in pollen per $cm^3$. Since the number of pine pollen grains per $cm^3$ does not decrease (Davis, 1975), lower pine pollen frequency following the introduction of grazing probably results from range deterioration and increased non-arboreal pollen production. The deposition of large numbers of long-distance transported pine pollen (Mack and Bryant, 1974) seems to have remained fairly constant at Wildcat Lake.

The plant families and genera (Tubuliflorae, Chenopodiaceae, Cruciferae, *Ambrosia,* and *Erodium*), whose pollen percentages increase above 0.40 m, contain many weedy species. Presumably, weeds were able to invade degraded range land. Cheno-ams are the most abundant (47 percent) pollen type at the top of the core. Weedy Chenopodiaceae currently growing in the area include *Chenopodium album, Salsola kali,* and *Kochia scoparia.* Although we do not know when these species entered southeastern Washington, they were first collected around the turn of the century. *Chenopodium album* was collected in 1885 (W.S.U. Herbarium No. 145462), *Salsola kali* in 1901 (Herbarium No. 145421), and *Kochia scoparia* in 1906 (Herbarium No. 195444). *Erodium cicutarium* and several species of Cruciferae *(e.g., Alyssum alyssoides, Lepidium perfoliatum,* and *Sisymbrium altissimum)* are invaders of disturbed range land and are common in the Wildcat Lake area today.

Two periods of intense disturbance recorded in sediments at 0.38 and from 0.17 to 0.20 m are typified by very low organic-matter weight-loss, lower pollen concentration per $cm^3$, high fungal spore concentration per $cm^3$ (Davis, 1975), and high percentages of pollen from genera with low pollen production and/or poor dispersal (Cruciferae and *Erodium*). Increased erosion associated with intense overgrazing represented at 0.38 m appears to have produced faster deposition, which reduced the pollen concentration per $cm^3$ and decreased sediment organic content. Cruciferae and Tubuliflorae pollen was washed, with silt, into the lake.

Fungal spores, first abundant at 0.50 m, reach a submaximum at 0.38 m (Davis, 1975). The most abundant type is *Sporormiella,* a dung inhabiting genus of ascomycetous fungi. *Sporormiella* spores appear to be particularly important indicators of grazing pressure. Their abundance in the lake sediments probably depends on the availability of fecal matter from grazing herbivores, and on slope-wash resulting from overgrazing. This proposed range destruction may correlate with overgrazing by horses in the 1890's (Cotton, 1904).

At 0.20 m the organic matter percent again decreases, the number of pollen grains per $cm^3$ drops, and fungal spores reach their highest values (Davis, 1975). This period of intense disturbance may differ from the earlier period because of (1) different effects of grazing, first by horses and then by sheep, (2) the abundance of introduced weeds during the second interval, (3) intensive use only during winter months from 1905 to 1920, and (4) differences in climate between the two periods.

Above 0.20 m the percent organic-matter weight-loss rises, there are fewer fungal spores, less Cruciferae and *Erodium* pollen, and a few *Botryococcus* microfossils reappear. Possibly these recent changes reflect enlightened grazing practices and/or increased effective precipitation since the 1920's.

#### Summary

Although terrestrial pollen percentages are relatively stable prior to the introduction of horses, sheep, and cattle, changes occurred in the Wildcat Lake aquatic environment following deposition of Mt. St. Helens W volcanic ash. Two periods of intense erosion followed the introduction of grazing and subsequent range deterioration. It is obvious from these studies at Wildcat Lake that no climatic event of the past 1000 years has resulted in vegetation changes as great as those brought about by European agricultural and grazing practices.

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# Hydrogen Sulfide Fumes at the Summit of Mount Rainier Volcano, Washington

**Abstract**

Numerous small fumaroles occur on the rims and floors of the two summit craters of Mount Rainier volcano, but present $H_2S$ emission is restricted to certain fumaroles along the west rim of the west crater and in a large west crater ice chamber called the Lake Grotto. A concentration of 57.3 ppm $H_2S$ was measured in one Lake Grotto fumarole and 3.8 ppm in the Lake Grotto atmosphere. Increased $H_2S$ concentrations can precede eruptions by a few months or years and could furnish an extremely useful method of monitoring volcanic activity.

Slow enlargement of the Lake Grotto and a similar chamber in the east crater since at least 1971 indicates that heat flow has recently increased. The remainder of the 2,200 m long geothermal ice cave system, as well as the surface of the overlying crater ice fill, have remained virtually constant in appearance. Thus, they are in dynamic equilibrium with geothermal heat release, the rate of melting of the cave walls and ceiling, the slow subsidence of the ice masses that fill the craters, and the annual accumulation and ablation of snow at the surface.

## Introduction

A portable gas analysis device purchased with research funds from the Mazamas was used in August 1975 to measure hydrogen sulfide ($H_2S$) fumes at selected sites in the summit craters of Mount Rainier volcano. Sulfur odors were locally intense and "nauseating" when Stevens and Van Trump made the first authenticated climb of the 4,393 m high mountain (Stevens, 1876, p. 526). The west crater fumarole that they huddled around on the night of August 17, 1870, may have been one of several on the west rim of the west crater currently emitting detectable sulfur odors. However, the strongest sulfur odors originate from a fumarole cluster on the floor of the Lake Grotto (Fig. 1). Sulfur fumes are also occasionally noted at about 3,990 m elevation on the Ingraham Glacier where they emanate from crevasses.

Although the locations of sulfurous fumaroles were noted in 1971 when the Lake Grotto was first explored and mapped (Kiver and Steele, 1972), no attempt at quantitative analysis was made until the summer of 1975 when two of us (Snavely and Snavely) spent seven days at the summit. Subsequent measurements will determine if, and how much, $H_2S$ composition varies during the present repose period. Significant increases in sulfur, $H_2S$, and other gases have occurred prior to volcanic eruptions (Sato and others, 1975; Tonani, 1972). If this increase also occurs at Mount Rainier, then a useful tool for predicting its eruptions could be established.

## Methods and Materials

A detector tube system was used for the analysis because it is lightweight, compact, easy to use, and gives immediate quantitative results after simple elevation and gas tempera-

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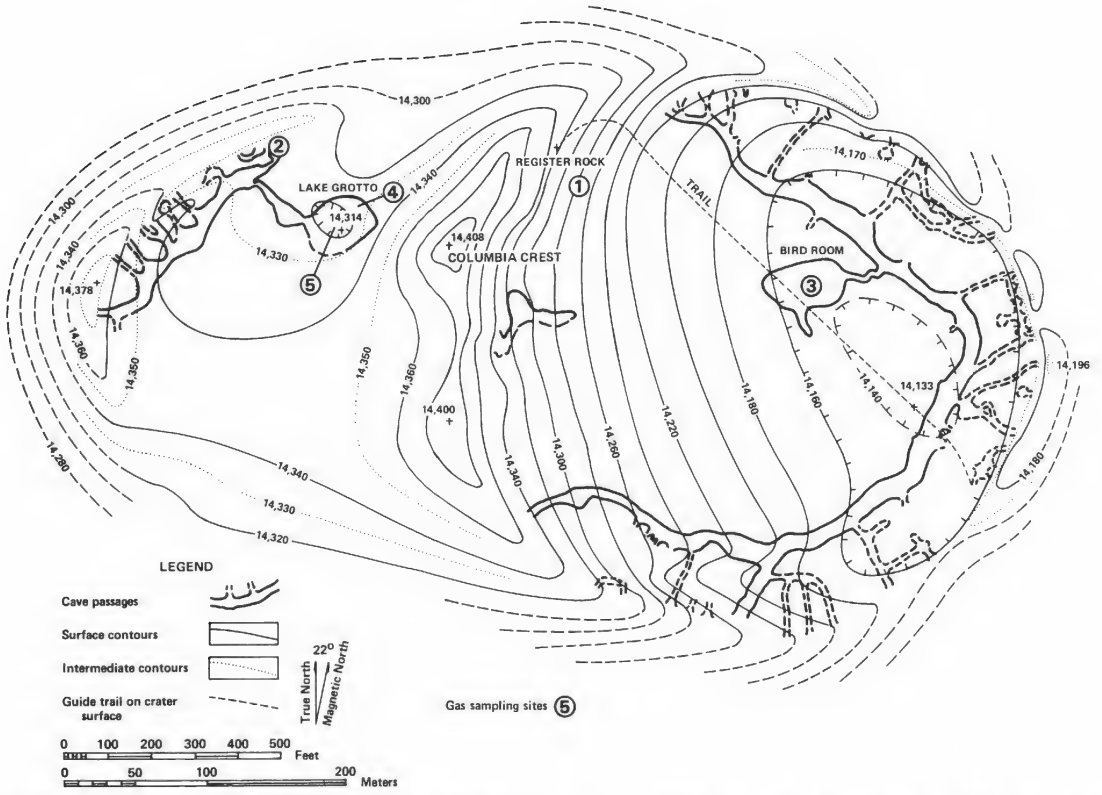


Figure 1. Map showing the topography and cave locations as they existed in 1971. Present conditions are virtually the same except that the Lake and Bird Grottoes have enlarged and the depression in the ice above the Lake Grotto has subsided 10 m to an elevation of approximately 4,388 m (14,304 ft). Art work by Fred Munich.

ture corrections are made. A detector tube is a sealed glass tube containing chemical reagents and is most often used in air pollution studies. The tube tips are broken off before an analysis and the tube is inserted into a pump that draws a known quantity of gas through the reagents. The length of the colormetric reaction of the reagents is then proportional to the concentration of a specific gas. For example, $H_2S$ reacts with cupric sulfate ($CuSO_4$) to form blackish, brown-colored cupric sulfide (CuS).

The accuracy is within $\pm$ 25 percent of true value where interfering gases such as $SO_2$ are minor and the temperature of the detector tube is held between 0 and 40°C. Multiple analyses of a single fumarole usually give results reproducible to within 10 percent. Numerous detector tubes that measure other gases are manufactured, but were unavailable to us during the expedition. We believe that our $H_2S$ and CO measurements at least give reasonable order-of-magnitude estimates.

Some error may have been introduced by measuring fumarole gases with temperatures as high as 80°C. The samples were taken relatively quickly, so that the tube and reagent temperatures were probably never in excess of the 40° C maximum recommended by the manufacturer. If $SO_2$ concentrations exceed 0.5 percent, then some error in the $H_2S$ measurements will occur. Although $SO_2$ was not measured at Mount Rainier, measurements at Mount Baker (Kiver and Steele, unpublished) and Mount Hood (Phillips, 1935) suggest that $SO_2$ is absent or very minor in Cascade volcanoes. A laboratory analysis using a Naugton tube (Fuilayson, 1972) or other reliable sampler is needed so that the results of different analytical methods can be compared.

### Results and Discussion

Gas sample sites at the crater surface (site 1) and in the caves (sites 2, 3, 4, and 5) are shown in Figure 1 and temperature and gas composition in Tables 1 and 2. Site 3 is the cave atmosphere in the large east crater Bird Room that measures 54 x 36 m in area

TABLE 1. Fumarole and/or Air Temperature (°C)

| Site | Fumarole Temperature | Air Temperature |
|---|---|---|
| 1 | 80 | 0 |
| 2 | 70 | 0 |
| 3 | *NA | 8 |
| 4 | *NA | 5 |
| 5 | 73 | 5 |

*Not applicable; cave air sample

TABLE 2. Fumarole or Air Composition by Volume (PPM)

| Site | CO[a] | CO[b, c] | $H_2S$[a] | $H_2S$[b] |
|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 |
| 2 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0 | 0 | 0 |
| 4 | 0 | 0 | 2.0 | 3.3 |
| 5 | 2 | 3.8[d] | 20.0-30.0 | 38.2-57.3[c] |

(a) Not corrected for elevation and temperature
(b) Corrected for elevation
(c) Corrected for temperature
(d) Value is probably in error, see text for explanation

and 21 m high, and site 4 is the cave atmosphere in the west crater Lake Grotto, an irregular ovoid measuring 52 m x 41 m and 10-14 m high. The floors of the Bird Grotto and the Lake Grotto are 98 m and 39m, respectively, beneath the surfaces of the overlying ice.

Gases from numerous fumaroles, as well as slowly circulating surface air, mix in these large cave rooms and allow average gas composition for the lower sections of the caves to be determined. The rooms are ideal sites for monitoring long-term changes in volcanic emanations because they are relatively easy to find, and their narrow connections with upslope cave passages prevent rapid mixing with outside air. Disadvantages are that increased volcanic emissions may allow gases in toxic concentrations to accumulate; and, secondly, increases in volcanic emissions are often accompanied by thermal increases that could cause considerable enlargement or collapse of the upslope connecting passage, or cause the ice ceilings to melt completely, thereby permitting rapid mixing with outside air.

Indeed, slow enlargements of the Bird and Lake grottoes since they were first entered in the early 1970's is probably due to small, recent heat increases. A depression in the ice surface above the slowly enlarging Lake Grotto has deepened from 5 m in 1971 to 15 m in 1975 and provides the first surface indication of cave enlargement. The remainder of the 2,200 m long geothermal ice cave system, as well as the surface of the ice that fills the summit craters, is unchanged.

The relatively constant level of ice fill from year to year since at least 1970 indicates that snowfall at the summit is more than adequate, even in extremely light snowfall winters like 1972-73, to fill the craters to normal snow level. Ablation has not been excessive during this period of time; thus, the observed changes in the caves and the deepening surface depression are not climatically caused.

The caves themselves furnish a means of monitoring volcanic heat release because a dynamic equilibrium normally exists between the amount of heat released, the rate of melting of the cave walls and ceiling, the slow subsidence of the ice masses that fill the craters, and the annual accumulation and ablation of snow at the surface (Kiver and Steele, 1975a). Changes in the morphology of the caves or the surface of the ice fill imply a change in one or more of these controlling factors.

CO at the summit is absent except possibly at site 5. However, the presence of $H_2S$ at site 5 invalidates the CO test there because both $H_2S$ and CO cause a similar stain in the potassium palladosulfite used as a reagent.

$H_2S$ emission is presently low and restricted to the west crater. The 3.8 ppm in the west crater cave atmosphere is within the recommended 10 ppm limit for an average 8-hour exposure in industrial situations and requires no special breathing apparatus.

High concentrations of $SO_2$ or $NO_2$ gases could cause errors in $H_2S$ measurements. Judging from our unpublished analyses and the preliminary analyses of Motoari Sato (pers. comm.) of the fumarole gases at Mount Baker, as well as analyses at Mount Hood (Ayres and Cresswell, 1951; Phillips, 1935), $SO_2$ and $NO_2$ are absent or relatively unimportant in Cascade volcanoes.

$H_2S$ measurements of fumaroles at Mount Baker volcano, 208 km north of Mount Rainier, before and during the steam eruption that was first noted on 10 March 1975, showed a dramatic increase from .0074 percent during August 1974, to slightly greater than .15 percent on 31 March 1975, to 6.0-7.4 percent in September 1975 (Kiver and

Steele, 1975b). At this writing it remains to be seen whether the dramatic increase in $H_2S$ concentration and steam activity at Mount Baker presages a more serious eruption.

With the exception of Lassen Peak, there has not been a Cascade eruption since the 19th century. The repose period of one or more of these volcanoes will probably terminate in the near future, making documentation of gas composition, temperature, micro-seismic activity, and other parameters an important goal. Gathering a maximum amount of scientific data soon, coupled with continuous or nearly continuous monitoring when possible premonitory signs develop, may determine important eruption prediction criteria.

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# Agonistic Behavior in Uinta Ground Squirrels

**Abstract**

A modified "arena" technique was used on an unconfined population of Uinta ground squirrels *(Spermophilus armatus)* in Grand Teton National Park to study the structure of agonistic interactions. In late summer, 1969, 213 encounters were observed. Six major postural components were identified and described: initial contact, threat, attack, combat, submission, and escape. Encounters were rapid, complex, and brief; they were divided into: approach, contact, and break of contact. Flow diagrams are given for the 213 interactions. Most terminated (ca 75 percent) at the conclusion of a threat-submission interaction, but sometimes continued through fights and chases. The most severe forms of fights (locked) occurred in only 11 percent of the cases observed. The threat-submission postures permitted agonistic interactions to operate on a visual level to maintain social dominance with a minimum of physical contact.

Age and sex classes of Uinta ground squirrels have different times for entering hibernation, ranging from mid- to late summer each year (Slade and Balph, 1974; Costain, 1975, pers. comm.). Adult females disappear first, followed by males, females, and later by young of the year. Social organization at this time is in a state of flux as a result of the vacuum created by disappearing adults and maturation of young squirrels. This study examined the structure of agonistic behavior in a free-living population of Uinta ground squirrels during the terminal part of their annual above-ground activity cycle.

## Study Area

This study was conducted in the northern part of Jackson Hole, Wyoming, in Grand Teton National Park. This area has been described by Reed (1952), and by Craighead and Craighead (1952). Elevation is about 1900 m. The climate is characterized by long cold winters, deep snows, a short growing season, and low mean annual temperatures. Dice (1943) classified the area into the "Mountain Biotic Province." Vegetation is a mixture of grasses, forbs, and shrubs.

## Methods of Investigation

Since vegetation height and density precluded a direct investigation of agonistic interactions and their role in social organization, a modified "arena" technique (after Grubitz, 1966) was used. His closed arena involving paired squirrels was used in an investigation of agonistic behavior of six ground squirrel species. In order to draw squirrels into an area of unobscured view in this study, a food source was placed in an area of high squirrel density. The food source was a can, full of sorghum and Purina rabbit chow, buried to the level of the top of the can. Presumably this provisioning technique, similar

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to that used in numerous primate and other studies, did not alter the form of agonistic interactions although it probably did increase the frequency of such interactions. Competition over food provided an opportunity to observe agonistic interactions in a population unrestricted in its movements.

Preliminary observations located a site containing at least 13 squirrels. A catalogue of agonistic behaviors was made during June, 1969, on these 13 animals and squirrels at five other nearby locations. The principal study site was located on the periphery of Jackson Hole Biological Research Station where squirrels were somewhat habituated to humans. Park philosophy precluded individually marking squirrels. Obervations were made from a blind about 4 m from the food can. Squirrels were watched at various intervals from 9 AM to 1 PM daily for 22 days (7 July to 19 August, 1969) until the last squirrel in the area disappeared below ground for the year. In 1969, Costain (1975, pers. comm.) conducting a long-term ecological study of this population, trapped the last adult male on 31 July, the last adult female on 2 August, and the last young on 24 August; the last young seen was on 30 August. Observations averaged 109 minutes each day, and 2,410 minutes for the entire study; 213 agonistic interactions were observed. An Agfa Optima 500 (55 mm lens) and a Kodak Super 8 movie camera were used to supplement observations. Supplementary observations were made at several locations in western Wyoming in the summer of 1974.

#### Agonistic Behavior Patterns

Agonistic behavior patterns were divided into six major components (Fig. 1). The classification scheme is an expansion of that used by Ralph and Stokes (1963) and Burns (1968); it also includes information from Grubitz (1966) and Eisenberg (1968).

*Initial Contact.* The first physical contact between squirrels was usually in the forms of: 1) Naso-Nasal Contact in which squirrels touch noses, vibrissae, or mouths; or 2) Naso-Anal Contact in which sniffing or licking the other squirrel's genital region was involved.

*Threat.* Postural components include open mouth, a semi-arched back, forelegs flexed, hind legs extended, tail held to one side, tail hairs erect and head towards the opponent.

*Attack.* An attacking squirrel lunges forward directly at the focus animal, usually striking the opponent with its limbs, body or teeth.

*Combat.* Behavior of combatant squirrels involved prolonged physical contacts; these took the forms of: 1) Locked Fights, in which squirrels oriented themselves with ventrums pressed together while rolling about biting at each other; 2) Modified Fights, in which a squirrel exhibited an attack lunge involving brief physical contact followed by immediate separation; and 3) Boxing, in which squirrels stand upright on hindlegs with forepaws held towards each other. Striking or sparring occurs.

*Submission.* Submission lacks all postural components of threat; the head may be raised or held flat against the substratum, shoulders are low, and tail is straight or slightly lifted above the substratum. The squirrel frequently remains motionless in this posture with its legs flexed and its eyes half closed.

*Escape.* Withdrawal from an agonistic interaction involves a rapid locomotion away

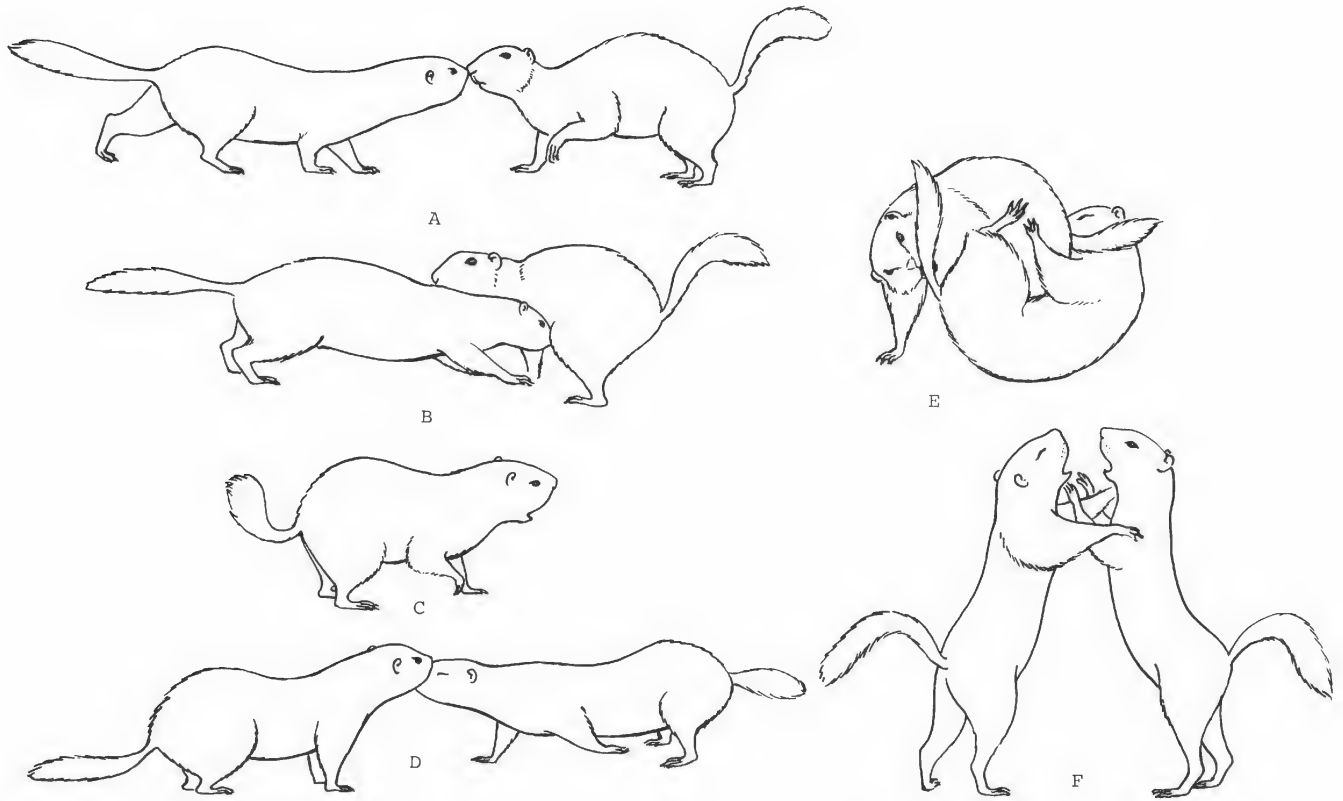


Figure 1. Postures observed in agonistic interactions among Uinta ground squirrels. A: Naso-nasal contact, B: Naso-anal (genital) contact, C: Threat, D: Dominant-subordinant interaction, E: Locked fight, and F: Boxing.

from the opponent. The retreat terminates when the escaping squirrel enters a burrow, or when it disappears into the vegetation, or when the opponent stops chasing it. Distances between squirrels is relatively uniform throughout the chase and rarely exceeds a meter.

#### A Generalized Agonistic Interaction

Agonistic interactions were divided into: 1) approach, 2) contact, and 3) break of contact, although in reality these form a continuum (Grubitz, 1966). Encounters are rapid, complex, and brief, usually less than a minute.

*Approaches.* Most agonistic interactions started when a squirrel approached an animal eating at the food can. The approaching squirrel frequently moved in a slow, jerky locomotion; tail movements took no apparent pattern as squirrels approached. When the approach was from a posterio-lateral to posterior direction relative to the squirrel at the food can, the eating squirrel sometimes whirled around to face the oncoming animal. The approaching squirrel, if unchallenged, moved directly to the food can and the two animals began eating side-by-side. An agonistic behavioral sequence usually ensued if a challenge by either squirrel was given; these sequences comprised some or all of the behavioral categories defined above.

*Contact.* Initial contact generally consisted of either a Naso-Nasal or Naso-Anal posture. A few instances were observed in which two squirrels approached head on and moved side-by-side, each facing head-to-tail. Other types of contact sometimes followed, including Combat behavior involving Locked Fights, Modified Fights, and Boxing. Any interaction may have exhibited all or part of these behavior patterns.

*Break of Contact.* Termination of contact occurred when one squirrel turned and ran (Escape), usually being chased. The pursuing squirrel persisted in the chase only a short distance before returning to the food can or to other activities.

#### Agonistic Behavioral Sequences

A flow diagram showing the sequences of 213 agonistic interactions is given in Figure 2. Initial contacts were either Naso-Nasal (25 percent), Naso-Anal (36 percent), or Neither (40 percent). The "Neither" category included a situation in which one squirrel was eating at the food can and another squirrel approached and immediately began eating.

After the initial contact, one of the squirrels usually threatened the other (54 percent), submitted (27 percent), or escaped (19 percent). If one squirrel threatened the other, the interaction usually continued. If one squirrel submitted, the agonistic encounter was terminated: the two squirrels ate side-by-side, or if one squirrel escaped, the remaining one stayed and ate alone.

When interactions continued, some squirrels responding to the threat submitted (16 percent), some type of combat ensued (54 percent), or one of the squirrels escaped (30 percent) (Fig. 3). If one squirrel submitted or escaped, this terminated the interaction. Combat took the form of locked fights (39 percent), modified fights (35 percent), or boxing (26 percent). The interaction may then have terminated if one or both squirrels began eating (11 percent). If one squirrel escaped (89 percent), however, the encounter ended with that individual's retreat (71 percent) or with the other ani-

mal giving chase (30 percent). In half of the locked fights and all boxing bouts, vocalizations were heard. Chases (N=16) seldom persisted over 5 m (N=2).

### Contacts and Responses

The types of initial contact varied slightly, but differences were not significant. Responses also varied. A threat, as opposed to submission or escape, most often ensued

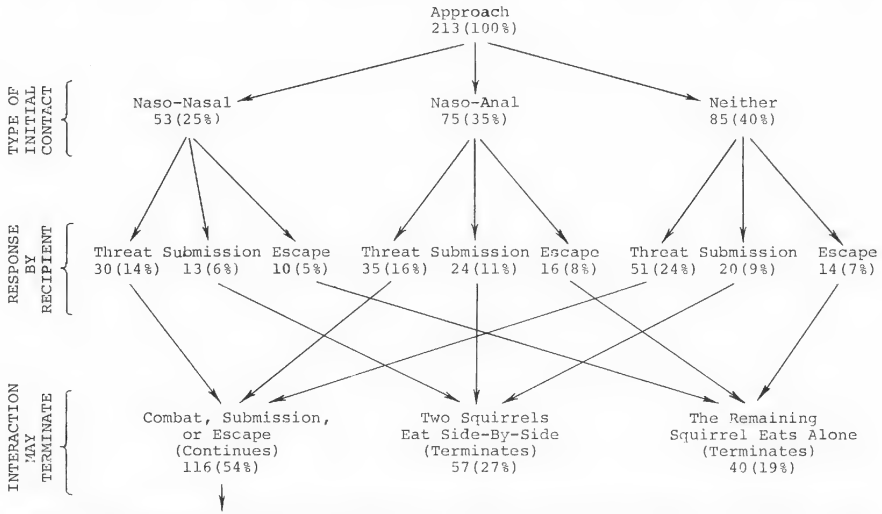


Figure 2. Flow diagram showing the behavioral sequences comprising agonistic interactions in the Uinta ground squirrel.

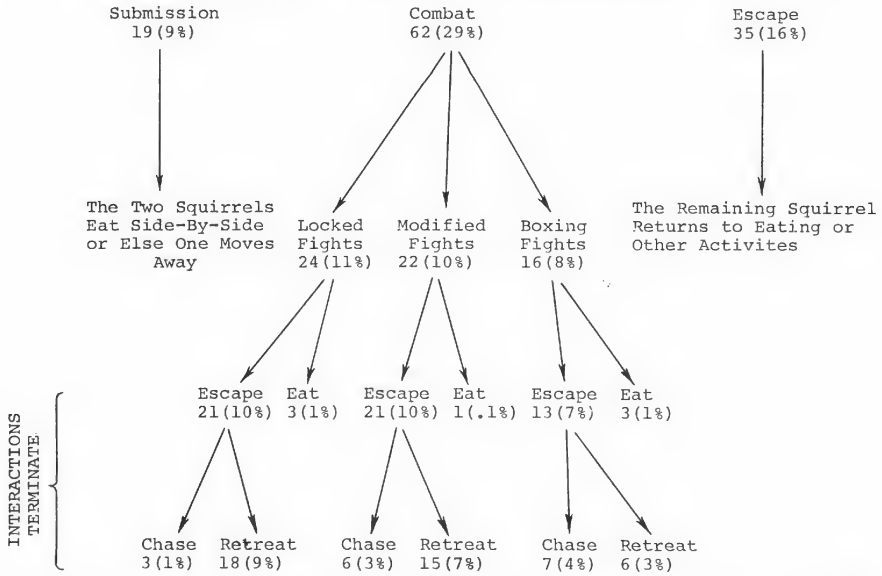


Figure 3. Flow diagram showing the behavioral sequences most agonistic interactions took in Uinta ground squirrels, if they did not terminate at an early "stage" shown in Figure 1.

after the initial contact; this difference was significant ($X^2$=16.2, 2df; p=.001). Threats most often led to combat (62 percent) rather than submission (16 percent) or escape (22 percent); this difference was also significant ($X^2$=24.1, 2 df; p=.001). Combative behavior took three forms (Fig. 2); differences were not significant. These interactions terminated in either an escape by one squirrel, which may be chased (29 percent) or both squirrels starting to eat; differences between escaping and eating were significant ($X^2$=27.6, 1df; p=.001).

#### Discussion

Agonistic interactions are highly variable in Uinta ground squirrels. Usually encounters terminated at the conclusion of a threat-submission interaction, but sometimes continued through fights and chases. About one-fourth of all interactions involved combat; the most severe form of fights (locked) occurred in only 11 percent of the cases observed. The outcome of most combats was apparent when one squirrel retreated. Dominance-subordinance hierarchies were established with little overall physical contact and possible injury to each other.

Since ground squirrels are diurnal, a large part of agonistic behavior is based on visual exchanges of information between potential opponents (Grubitz, 1966). Perhaps most individuals were littermates or neighbors and had probably encountered each other numerous times and in a variety of circumstances before our study. The food can "arena" probably served only to intensify the agonistic interaction rate among these young squirrels.

Burns (1968) found that, in the same season as our study, most Uinta ground squirrels in his Utah population seemed to maintain individual distances of tolerance; they became aggressive towards other squirrels that approached to within 0.6-1.5 m of them. Large numbers of young Uinta ground squirrels disappeared from his population during this season. Burns noted that the period of disappearance is characterized by instability in the population resulting from: 1) development of sexual behavior; 2) increased aggression in one-year-old males and young females; and 3) increased movement by young that were lost during this period when young females dominated over males. This disproportionate disappearance seemed directly related to aggression on the part of young females in the Utah population. Presumably this fact has adaptive significance in that young females consequently remained in areas that already had proved themselves to be consistently productive environments. When these young females then emerged from hibernation the following spring, they would already inhabit such an area.

The complex sequence of agonistic behavior patterns served to establish or reinforce social dominance among Uinta ground squirrels. The threat-submission postures permitted the interactions to operate on a visual level to maintain social dominance with a minimum of physical contact.

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# Occurrence of the Shorthead Sculpin, Cottus Confusus, in a Headwater Tributary of Deschutes River, Washington

**Abstract**

Five specimens of the shorthead sculpin *(Cottus confusus)* have been collected from Hard Creek, a cold-water tributary of the upper Deschutes River in western Washington. They represent the first recorded occurrence of this species from a southern Puget Sound river system, and their presence above the barrier falls of Deschutes River suggests that the shorthead sculpin invaded the Puget Sound region earlier than had previously been believed.

The shorthead sculpin, *Cottus confusus,* is a cold-loving species that prefers fast-flowing streams fed by snow melt or cold springs (Bond, 1963; Reimers and Bond, 1967). In the Puget Sound region this sculpin has been reported by McPhail (1967) to inhabit eastern drainages from Skykomish River south to Green River as well as some small streams in the Kitsap Peninsula on the west side of the sound (Fig. 1). Neither Bailey and Bond (1963) nor McPhail (1967) noted its presence in rivers entering the southern part of Puget Sound.

Five specimens of *C. confusus* (Table 1) were collected by electrofishing in Hard Creek, Lewis Co., Washington (T14N-R3E-Sect. 13) on 23 October 1975. Hard Creek is a small spring-fed Deschutes River tributary entering the river 12.7 km upstream from Deschutes Falls, an impassable barrier located 66.1 km from the river mouth. The collection site is characterized by a steep gradient with many debris dams, dense canopy, and cold water. Temperatures in Hard Creek have not been recorded in excess of 13 C. No other fishes were observed. Part of an adjacent stream (Ware Creek) from which most streamside vegetation had been removed was found to contain numerous cutthroat trout *(Salmo clarki)* but no sculpins; but Thurston Creek, a somewhat larger tributary entering the Deschutes 2.7 km downstream from Deschutes Falls, contained cutthroat trout, juvenile coho salmon *(Oncorhynchus kisutch),* and the torrent sculpin, *Cottus rhotheus.*

The external morphology of the specimens (Table 1) agrees in most respects with the description of the species given by Bailey and Bond (1963), although there appears to be a slight reduction in head size among the Hard Creek population. In addition, axillary prickling is poorly developed in each of the specimens, a feature associated by Bailey and Bond with certain other isolated populations.

The presence of *C. confusus* above the barrier falls of Deschutes River necessitates a re-examination of its distributional history in western Washington. Bailey and Bond (1963) believe that *C. confusus* first entered Puget Sound by crossing into the South Fork of the Snoqualmie River from the Yakima River, as it is the only sculpin present above Snoqualmie Falls. McPhail (1967) stated that this invasion took place during the late stages of glacial Lake Russell prior to entry of the sea into Puget Sound, because dispersal into the rivers of southern Puget Sound had apparently not taken place, nor had the species utilized the connection that once existed between Puget Sound and Che-

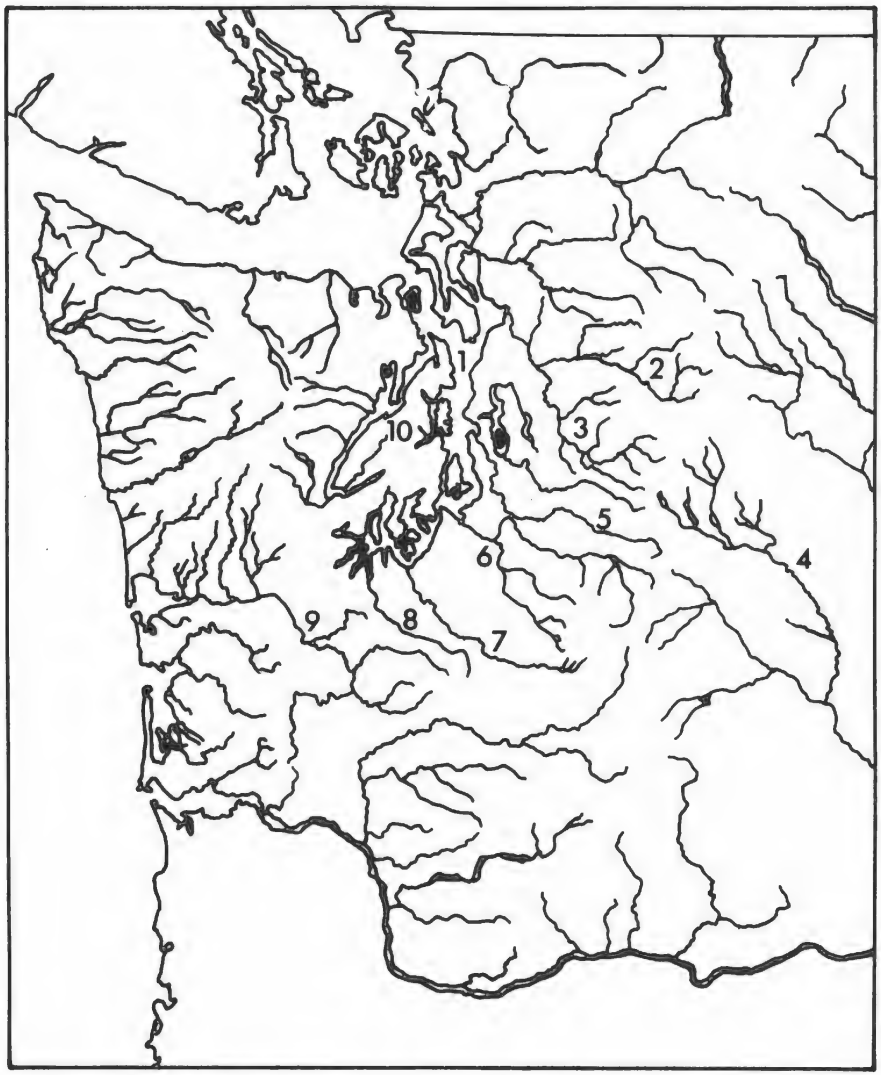


Figure 1. Location of drainage systems mentioned in the text. 1. Puget Sound, 2. Skykomish River, 3. Snoqualmie River, 4. Yakima River, 5. Green River, 6. Puyallup River, 7. Nisqually River, 8. Deschutes River, 9. Chehalis River, 10. Kitsap Peninsula.

halis River. However, the discovery of *C. confusus* in the headwaters of the Deschutes River indicates that the shorthead sculpin reached Puget Sound earlier than has previously been believed and has had time to spread to its southernmost river. An earlier invasion might also eliminate the need to postulate a crossing of Lake Russell from the eastern rivers to the Kitsap Peninsula (McPhail, 1967); an alternative explanation is that the species spread from stream to stream along the border of the Puget Sound glacial lobe and that the Kitsap Peninsula was last to be colonized. If this were the case, there is a

TABLE 1. Selected morphological features of five specimens of *C. confusus* (OS 5162) from Hard Creek, Deschutes River drainage. Morphometric measurements are expressed as a proportion of standard length.

| | | | | | |
|---|---|---|---|---|---|
| Standard Length (mm) | 79.7 | 65.8 | 66.6 | 46.8 | 36.5 |
| Total Length | 1.182 | 1.213 | 1.179 | 1.218 | 1.200 |
| Body Depth | .194 | .208 | .204 | .199 | .189 |
| Caudal Peduncle Depth | .084 | .093 | .096 | .088 | .080 |
| Caudal Peduncle Length | .146 | .187 | .110 | .171 | .170 |
| Predorsal Length | .315 | .318 | .306 | .314 | .337 |
| Highest Dorsal Spine | .084 | .079 | .078 | .068 | .080 |
| Highest Dorsal Soft Ray | .123 | .125 | .125 | .139 | .121 |
| Highest Anal Ray | .162 | .140 | .120 | .122 | .104 |
| Longest Pectoral Ray | .257 | .236 | .225 | .246 | .241 |
| Longest Pelvic Ray | .176 | .193 | .170 | .169 | .151 |
| Head Length | .291 | .284 | .282 | .278 | .274 |
| Head Width | .256 | .258 | .248 | .233 | .233 |
| Snout Length | .094 | .088 | .090 | .090 | .099 |
| Postorbital Head Length | .138 | .144 | .129 | .132 | .143 |
| Interorbital Width | .041 | .047 | .036 | .047 | .047 |
| Length of Upper Jaw | .142 | .121 | .117 | .096 | .088 |
| No. Dorsal Spines | 7 | 7 | 8 | 7 | 8 |
| No. Dorsal Soft Rays | 17 | 18 | 17 | 17 | 17 |
| No. Anal Rays | 13 | 13 | 12 | 13 | 13 |
| No. Pectoral Rays | 14 | 15 | 15 | 14 | 14 |
| No. Pelvic Rays | I,3 | I,4 | I,4 | I,4 | I,4 |
| No. Preopercular Spines | 2 | 2 | 2 | 3 | 3 |

definite possibility that *C. confusus* exists in suitable headwater areas of the Nisqually and Puyallup river systems, and perhaps also in the Chehalis River drainage.

**Acknowledgments**

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# Food Habits of Bats of Western Oregon[2]

## Abstract

Major foods by percentage volume in 239 stomachs of 11 species of bats from western Oregon were as follows: *Myotis lucifugus*—Chironomidae, internal organs of large insects, Diptera; *M. yumanensis*—Chironomidae, Isoptera, Lepidoptera; *M. evotis*—Lepidoptera, Diptera, Araneida; *M. thysanodes*—Lepidoptera, Phalangida; *M. volans*—Lepidoptera, Isoptera, Araneida; *M. californicus*—Chironomidae, Diptera, Tipulidae; *Lasionycteris noctivagans*—Lepidoptera, Isoptera, Diptera; *Eptesicus fuscus*—Lepidoptera, Scarabaeidae, Coleoptera; *Lasiurus cinereus*—Culicidae, Lepidoptera; *Plecotus townsendi*—Lepidoptera; *Antrozous pallidus*—Scarabaeidae, Tettigoniidae.

## Introduction

Published information is not available on the food habits of bats from Oregon or on food habits of the following species: *Myotis evotis, M. thysanodes, M. volans, M. californicus.*

The purpose of this paper is to present data on the foods eaten by 239 bats of 11 species occurring in western Oregon and eastward along the Columbia River from the coast to the vicinity of The Dalles.

## Methods and Materials

Bats were collected from mid-1970 through 1974 in mistnets from daytime roosts, and some were shot while foraging. Some bats were uncommon and/or difficult to secure whereas others had empty stomachs. This combination of factors accounts for the small sample-sizes for some species.

Stomach contents were preserved in 10 percent formalin. They were examined and identifications were made by comparison with whole items. Estimates were made of the percentage volume of each food in each stomach by visual observation using a 10- to 70-power zoom dissecting microscope.

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### Description of Study Area

Most of the bats in this study were captured along the Oregon coast from the Cascade Head Experimental Forest near Otis in Lincoln County southward to the California border (Maser and Franklin, 1974). The second largest number of specimens were collected along the Columbia River from The Dalles, Wasco County, westward to the coast. Additional bats came from the following locations: (1) vicinity of Ashland, Jackson County, (2) vicinity of Junction City, Lane County, (3) H. J. Andrews Experimental Forest, Lane County, on the western flank of the Cascade Mountain Range, and (4) vicinity of Corvallis, Benton County, including the William L. Findley National Refuge.

The localities in which the specimens were collected fall in the following major vegetational areas of Franklin and Dyrness (1973): (1) Oregon coast—Sitka spruce, *Picea sitchensis,* Zone, (2) Columbia River (beginning at the coast)—Sitka spruce Zone; Western hemlock, *Tsuga heterophylla,* Zone; Willamette Valley; Ponderosa pine, *Pinus ponderosa,* Zone, (3) Ashland—Mixed Conifer and Mixed Evergreen Zones, (4) Junction City and Corvallis—Willamette Valley, and (5) H. J. Andrews Experimental Forest —Western hemlock Zone.

### Results and Discussion

*Specific habitat and food considerations:*

*Myotis lucifugus,* Little brown myotis: The little brown myotis exhibited an affinity for forested areas, both coniferous and deciduous. These bats usually emerged about 20 to 30 minutes before full darkness and foraged among scattered trees and along edges of dense timber. They were often seen feeding in continuous circular patterns around buildings and small patches of trees, 5 to 10 ft above the ground.

The stomachs of 67 individuals were examined (Table 1). The most important foods in terms of percent volume were Chironomidae (adults and apparently some pupae), internal organs of larger insects (probably including many lepidopterans), unidentified Diptera, Isoptera (all Isoptera in all bats were the damp-wood termite, *Zootermopsis angusticollis*), and Trichoptera. Whitaker (1972) reported the top five foods by volume in 16 little brown myotis from Indiana to be Lepidoptera (21.6 percent), Trichoptera (13.1 percent), unidentified Diptera (11.9 percent), Cicadellidae (11.6 percent), and Delphacidae (8.8 percent). Only two of the foods, Diptera and Trichoptera, were among the top five items by volume in both Indiana and Oregon, and Cicadellidae formed only 0.4 percent of the volume in the Oregon material. Collectively, adult Diptera and Coleoptera in Indiana were 15.4 percent and 12.4 percent of the total volume. In Oregon individuals, corresponding values were 51.7 percent and 1.9 percent.

*Myotis yumanensis,* Yuma myotis: In western Oregon these bats were closely associated with large streams, rivers, ponds, or lakes. They normally emerged 20 to 30 minutes prior to full darkness and often fed just a few inches above the surface of the water, repeatedly flying regular routes. Along rivers and streams they flew up and down the stream in relatively straight patterns. Over ponds and small lakes they flew in circular patterns.

We examined 25 Yuma myotis stomachs (Table 1). Major foods by volume were Chironomidae, followed by unidentified tiny Diptera (probably including many chironomids), Isoptera, Lepidoptera, and internal organs of large insects. Other than for the Isoptera, these foods were similar to those reported for this species in Texas by Easterla and Whitaker (1972). They examined stomach contents of 14 individuals from

TABLE 1. Foods eaten by six species of myotis bats from western Oregon.

| Number examined / Item | *Myotis lucifugus* 67 | | *Myotis yumanensis* 25 | | *Myotis evotis* 13 | | *Myotis thysanodes* 4 | | *Myotis volans* 25 | | *Myotis californicus* 31 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. |
| Diptera (flies) | | | | | | | | | | | | |
| Chironomidae | 38.4 | 62.7 | 37.7 | 60.6 | — | — | — | — | — | — | 24.0 | 35.5 |
| Unidentified | 10.4 | 28.4 | 14.8 | 36.0 | 12.3 | 23.0 | — | — | 1.4 | 8.0 | 16.8 | 38.7 |
| Tipulidae | 2.4 | 7.5 | — | — | — | — | 6.3 | 25.0 | 0.2 | 4.0 | 15.6 | 25.8 |
| Culicidae | 0.4 | 1.5 | — | — | — | — | — | — | — | — | 3.2 | 6.5 |
| Dipterous larvae | 0.1 | 1.5 | — | — | — | — | — | — | — | — | — | — |
| Mycetophilidae | — | — | — | — | — | — | — | — | — | — | 0.6 | 3.2 |
| Psychodidae | — | — | 0.4 | 4.0 | — | — | — | — | — | — | — | — |
| Insecta, internal organs | 10.6 | 11.9 | 5.8 | 12.0 | — | — | — | — | — | — | — | — |
| Isoptera (termites) | 8.9 | 13.4 | 18.8 | 32.0 | 3.1 | 7.7 | — | — | 7.6 | 12.0 | 4.8 | 9.7 |
| Trichoptera (caddisflies) | 8.4 | 10.4 | — | — | — | — | — | — | — | — | 4.7 | 6.5 |
| Insecta, unidentified | 6.3 | 26.9 | 4.2 | 24.0 | 1.5 | 7.7 | — | — | 0.4 | 8.0 | 4.2 | 12.9 |
| Lepidoptera (moths) | | | | | | | | | | | | |
| Unidentified | 3.7 | 10.4 | 14.8 | 32.0 | 46.2 | 84.6 | 46.2 | 75.0 | 78.2 | 88.0 | 14.4 | 25.8 |
| Lepidopterous larvae | 1.4 | 1.5 | — | — | — | — | — | — | — | — | — | — |
| Hymenoptera (bees & ants) | | | | | | | | | | | | |
| Formicidae | 2.3 | 6.0 | — | — | — | — | — | — | — | — | — | — |
| Unidentified | 0.4 | 1.5 | — | — | 4.2 | 15.4 | — | — | — | — | 0.6 | 3.2 |
| Coleoptera (beetles) | | | | | | | | | | | | |
| Scarabaeidae | 1.5 | 1.5 | — | — | 6.5 | 7.7 | — | — | — | — | — | — |
| Unidentified | 0.4 | 3.0 | 1.6 | 8.0 | 10.0 | 15.4 | — | — | — | — | 0.3 | 3.2 |
| Chrysomelidae | — | — | — | — | 1.5 | 7.7 | — | — | — | — | — | — |
| Hemiptera (true bugs) | | | | | | | | | | | | |
| Unidentified | 1.5 | 3.0 | 0.8 | 8.0 | — | — | — | — | 0.2 | 4.0 | 0.6 | 6.5 |
| Miridae | — | — | — | — | 3.8 | 15.4 | — | — | — | — | — | — |
| Pentatomidae | — | — | — | — | — | — | — | — | 1.4 | 4.0 | 1.0 | 6.5 |
| Homoptera (hoppers) | | | | | | | | | | | | |
| Cercopidae | 1.0 | 1.5 | 0.2 | 4.0 | — | — | — | — | — | — | 0.3 | 3.2 |
| Cicadellidae | 0.4 | 3.0 | — | — | 1.2 | 7.7 | — | — | 1.8 | 8.0 | 0.3 | 3.2 |

TABLE 1. (Continued)

| Number examined / Item | *Myotis lucifugus* 67 | | *Myotis yumanensis* 25 | | *Myotis evotis* 13 | | *Myotis thysanodes* 4 | | *Myotis volans* 25 | | *Myotis californicus* 31 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. |
| Unidentified | 0.4 | 1.5 | — | — | — | — | — | — | — | — | — | — |
| Aphididae | — | — | 0.1 | 4.0 | — | — | — | — | — | — | — | — |
| Orthoptera (crickets) | | | | | | | | | | | | |
| Tettigonidae | 0.5 | 1.5 | — | — | — | — | — | — | — | — | — | — |
| Gryllidae | 0.1 | 1.5 | — | — | — | — | 16.3 | 25.0 | 4.0 | 4.0 | — | — |
| Unidentified | — | — | — | — | — | — | — | — | — | — | 1.1 | 3.2 |
| Neuroptera (lacewings) | | | | | | | | | | | | |
| Hemerobiidae | 0.4 | 1.5 | — | — | — | — | — | — | — | — | — | — |
| Arachnida (harvestmen & spiders) | | | | | | | | | | | | |
| Phalangida | — | — | — | — | — | — | 26.2 | 50.0 | — | — | — | — |
| Araneida | — | — | 0.8 | 4.0 | 9.6 | 23.0 | 5.0 | 25.0 | 4.8 | 8.0 | 7.3 | 16.1 |
| | 99.9 | | 100.0 | | 99.9 | | 100.0 | | 100.0 | | 99.8 | |

Big Bend Park, Texas, and found small moths were the most important item, comprising 39.4 percent of the volume, followed by Chironomidae at 12.9 percent. The frequency of moths in stomachs was 78.6 percent and of chironomids was 42.9 percent.

*Myotis evotis,* Long-eared myotis: Although generally distributed throughout western Oregon, these bats were not abundant. They were associated with coniferous forest. Long-eared myotis emerged 10 to 40 minutes after full darkness and fed among the trees.

We examined 13 long-eared myotis stomachs during the present study (Table 1). The major food was Lepidoptera, which was found in 11 of the 13 individuals and totaled 46.2 percent of the volume. Other major foods were Diptera, Araneida, Coleoptera, and Hymenoptera. Isoptera occurred in one stomach.

*Myotis thysanodes,* Fringed myotis: Except in the Ashland area, fringed myotis are rare in Western Oregon. They appeared to be associated with coniferous forest. They emerged late, well after dark, but otherwise little is known about their foraging behavior.

Three of the four fringed myotis stomachs examined contained Lepidoptera, totalling 46.2 percent of the total volume (Table 1). Other foods were Phalangida (two stomachs, 26.2 percent), Gryllidae (one stomach, 16.3 percent), Tipulidae (one stomach, 6.3 percent), and Araneida (one stomach, 5.0 percent). In this species, three of the five foods —Phalangida, Araneida, and Gryllidae were or could be flightless forms. These totalled 47.5 percent of the volume. We suspect that a larger sample might have yielded less flightless forms.

*Myotis volans,* Long-legged myotis: These bats, generally distributed in the coniferous forest, were difficult to obtain. On warm, overcast evenings they fed along the edge of the forest and among the trees. On cold, clear evenings they were not seen, but may have been feeding within the forest. Emergence on heavily overcast evenings occurred as much as 45 minutes earlier than on lightly overcast evenings.

Relatively little diversity of foods occurs in this species (Table 1); 22 of the 25 bats contained small lepidopterans; 13 had only this food. Lepidoptera totalled 78.2 percent of the total volume. The only other foods that totalled over 2 percent of the volume were Isoptera (7.6 percent) and Araneida (4.8 percent) which occurred in three and two stomachs respectively.

*Myotis californicus,* California myotis: California myotis were abundant and generally distributed in western Oregon. They were easily obtained. Most individuals were collected from roosts under tarpaper siding on buildings.

Bailey (1936) stated that in Oregon these small bats began foraging about 15 to 20 minutes prior to full darkness. With one exception, we did not find California myotis to be active until after dark; consequently, we do not know where they were feeding. The exception was an individual shot as it foraged along the edge of timber 50 minutes before full darkness.

We examined 31 stomachs of *M. californicus* and found the top five foods to be Chironomidae, unidentified Diptera, Tipulidae, adult Lepidoptera, and Araneida (Table 1). California myotis was primarily a dipteran feeder; at least 60.2 percent of the total volume of food in our sample consisted of small flies. Isoptera and Trichoptera were important secondary foods. Except for the Araneida, all food items were flying forms.

Stanley G. Jewett, Jr. collected one of these bats feeding on "mayflies" along Fishhawk Creek near Jewell, Clatsop County, Oregon, at 1100 on 30 April 1955 (data from

specimen in Puget Sound Museum of Natural History). Krutzsch (1954) observed California myotis catching "oak moths" in California. The individual shot during the present study (10 miles E of Brookings, Curry County, Oregon, 13 April 1972) had a cranefly, Tipulidae, in its mouth.

*Lasionycteris noctivagans,* Silver-haired bat: Silver-haired bats were associated primarily with coniferous forest, but a few also were taken in mixed coniferous-deciduous forest. These bats were not abundant, but were generally distributed. Bailey (1936) maintained that silver-haired bats were late to emerge. We found them to emerge early, from 15 to 45 minutes prior to full darkness. These bats were the slowest-flying of the bats in Western Oregon. They frequently hunted in sweeping circles, often 100 yards or more in diameter. Although they normally foraged in and over the forest, they flew 20 to 40 ft above roads through the forest when such were available. Adults generally fed singly, but groups of three and four also were seen.

We examined 15 stomachs (Table 2). The most important food was adult Lepidoptera, totalling about a third of the volume. Isoptera were second in volume but only occurred in four individuals. The other top foods were unidentified Diptera (mostly tiny forms), unidentified insects, and Ichneumonidae.

There is little information in the literature concerning the food habits of this species. Whitaker (1972) examined two stomachs and found 95 percent Trichoptera and 5 percent Scarabaeidae. Gould (1955) found a stable fly, *Stomaxys calcitrans,* in the mouth of one, and Novakowski (1956) found young bats feeding on dipterous larvae at the bottom of the abandoned woodpecker hole in which they were living.

*Eptesicus fuscus,* Big brown bat: These bats occupied a wide variety of habitats, but were usually associated with coniferous and deciduous forest. They emerged early, frequently before the swallows had ceased to feed, 30 to 40 minutes before full darkness. They usually foraged high over the forest, in great sweeping circles sometimes well over 150 ft above the ground. As dusk deepened, however, they often descended to within 40 or 50 ft of the ground. When feeding along forest roads, big brown bats normally flew only 20 to 30 ft high and tended to fly relatively straight courses.

The stomachs of 30 big brown bats were examined (Table 2). The top five foods of this species were adult Lepidoptera, Scarabaeidea, Isoptera, Tipulidae, and unidentified Coleoptera. That adult lepidopterans were the top five (21.3 percent of the volume) is noteworthy since Hamilton (1933), Ross (1967), and Whitaker (1972) all indicated that adult Lepidoptera were not particularly important as food of big brown bats. Scarabaeid beetles were the second most important food by volume (18.3 percent) and Coleoptera, collectively, comprised 34.4 percent of the food volume. Isoptera formed 12.7 percent of the volume. Ross (1967) also found Isoptera to be food of big brown bats. Stinkbugs, Pentatomidae, made up only 1.3 percent of the volume in Oregon, but totalled 9.5 percent of the volume in Indiana (Whitaker, 1972). Non-flying insect foods were coleopterous larvae and Araneida.

*Lasiurus cinereus,* Hoary bat: These large, swift, late-flying bats appeared to be uncommon in western Oregon. They are associated with forested areas. The two specimens shot while foraging were flying in mixed coniferous and deciduous forest.

One stomach contained 100 percent adult mosquitos, Culicidae (Table 2). Many midges and other kinds of Diptera have been found in stomachs of bats, but very seldom mosquitos. The other stomach contained 100 percent Lepidoptera. Ross (1967) and Whitaker (1972) found Lepidoptera to be the important food of this species.

TABLE 2. Foods eaten by five species of bats from western Oregon.

| Number examined / Item | *Lasionycteris noctivagans* 15 | | *Eptesicus fuscus* 30 | | *Lasiurus cinereus* 2 | | *Plecotus townsendi* 16 | | *Antrozous pallidus* 11 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. |
| Lepidoptera (moths) | 32.0 | 53.3 | 21.3 | 50.0 | 50.0 | 50.0 | 99.7 | 100 | — | — |
| Isoptera (termites) | 14.0 | 26.7 | 12.7 | 20.0 | — | — | — | — | — | — |
| Diptera (flies) | | | | | | | | | | |
| Unidentified | 9.9 | 40.0 | 6.2 | 33.3 | — | — | — | — | 0.9 | 9.1 |
| Chironomidae | 3.0 | 6.7 | 0.7 | 3.3 | — | — | — | — | — | — |
| Culicidae | 2.0 | 6.7 | — | — | 50.0 | 50.0 | — | — | — | — |
| Mycetophilidae | 1.0 | 6.7 | — | — | — | — | — | — | — | — |
| Tipulidae | 1.7 | 13.3 | 6.8 | 16.7 | — | — | — | — | — | — |
| Rhagionidae | 1.3 | 6.7 | — | — | — | — | — | — | — | — |
| Muscoidea | — | — | 2.2 | 6.7 | — | — | — | — | — | — |
| Insecta, unidentified | 7.0 | 26.7 | 1.3 | 10.3 | — | — | — | — | 1.4 | 18.2 |
| Hymenoptera (bees and ants) | | | | | | | | | | |
| Ichneumonidae | 6.0 | 13.3 | 1.2 | 6.7 | — | — | — | — | — | — |
| Formicidae | 1.0 | 6.7 | — | — | — | — | — | — | — | — |
| Unidentified | — | — | 4.3 | 10.0 | — | — | — | — | — | — |
| Hemiptera (true bugs) | | | | | | | | | | |
| Pentatomidae | 5.3 | 26.7 | 1.3 | 10.0 | — | — | — | — | — | — |
| Unidentified | 1.3 | 6.7 | — | — | — | — | 0.3 | 6.7 | — | — |
| Coreidae | — | — | 0.3 | 3.3 | — | — | — | — | — | — |
| Orthoptera (crickets) | | | | | | | | | | |
| Gryllidae | 3.8 | 20.0 | 2.3 | 10.0 | — | — | — | — | 9.1 | 9.1 |
| Tettigoniidae | — | — | — | — | — | — | — | — | 17.3 | 18.2 |
| Trichoptera (caddisflies) | 2.7 | 6.7 | — | — | — | — | — | — | — | — |
| Coleoptera (beetles) | | | | | | | | | | |
| Scarabaeidae | 2.0 | 6.7 | 18.3 | 36.7 | — | — | — | — | 62.1 | 72.2 |
| Unidentified | 0.7 | 6.7 | 11.0 | 23.3 | — | — | — | — | — | — |
| Coleopterous larvae | — | — | 2.0 | 10.0 | — | — | — | — | — | — |
| Cerambycidae | — | — | 2.0 | 3.3 | — | — | — | — | — | — |
| Elateridae | — | — | 0.8 | 3.3 | — | — | — | — | — | — |

TABLE 2. (Continued)

| Number examined / Item | *Lasionycteris noctivagans* 15 | | *Eptesicus fuscus* 30 | | *Lasiurus cinereus* 2 | | *Plecotus townsendi* 16 | | *Antrozous pallidus* 11 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. | % vol. | % freq. |
| Chrysomelidae | — | — | 0.3 | 3.3 | — | — | — | — | — | — |
| Carabidae | — | — | — | — | — | — | — | — | 6.1 | 18.2 |
| Homoptera (hoppers) | | | | | | | | | | |
| Cicadellidae | 1.7 | 13.3 | 1.5 | 13.3 | — | — | — | — | — | — |
| Cercopidae | 1.7 | 13.3 | — | — | — | — | — | — | — | — |
| Arachnida (harvestmen & spiders) | | | | | | | | | | |
| Araneida | 1.3 | 6.7 | 2.8 | 3.3 | — | — | — | — | — | — |
| Acarina | 0.1 | 6.7 | trace | 3.3 | — | — | — | — | — | — |
| Neuroptera (lacewings) | | | | | | | | | | |
| Hemerobiidae | 0.3 | 6.7 | — | — | — | — | — | — | — | — |
| Insecta, internal organs | — | — | 0.5 | 3.3 | — | — | — | — | — | — |
| Chilopoda (centipedes) | — | — | — | — | — | — | — | — | 3.2 | 9.1 |
| | 99.8 | | 99.8 | | 100.0 | | 100.0 | | 100.1 | |

*Plecotus townsendi,* Western big-eared bat: These bats were normally associated with abandoned buildings and caves in western Oregon. Since all the bats in our sample came from day roosts, we do not know where they foraged; however, the roosts were associated with predominently coniferous forest.

Sixteen stomachs of this bat were examined and 15 contained only Lepidoptera (Table 2). The remaining stomach contained 95 percent Lepidoptera and 5 percent Hemiptera. Ross (1967) examined 38 digestive tracts of this species from Arizona and New Mexico and found the principal prey to be Lepidopterans.

*Antrozous pallidus,* Pallid bat: Pallid bats were late fliers. They emerged well after dark to forage within 2 to 5 ft above the ground, primarily near the edge of coniferous forests.

The 11 bats in our sample were collecred from a colony in the flue of a chimney and by mistnetting. Adult scarabaeids were the major food, forming 62.1 percent of the diet (Table 2). The only other important food was Tettigoniidae, forming 17.3 percent of the volume. Two foods, Chilopoda and Tettigoniidae, were probably captured on the ground or on vegetation.

Orr (1954) and Ross (1967) demonstrated that a wide variety of flightless, ground-dwelling forms are eaten, including small vertebrates.

*Comparative food considerations:*

Foods eaten by bats are greatly influenced by availability. However, there often are considerable differences in the food eaten by the different species. For example, *Myotis lucifugus, M. yumanensis,* and *M. californicus* fed heavily on Diptera, *Plecotus townsendi, Myotis volans, M. evotis,* and *Lasionycteris noctivagans* fed primarily on Lepidoptera, and *Eptesicus fuscus* and *Antrozous pallidus* on Coleoptera. There were also differences in usage within these groups. *Myotis lucifugus, M. californicus,* and *M. yumanensis* had similar food habits, but Isoptera and Lepidoptera were eaten much more often by *M. yumanensis* than by the other two. *Myotis lucifugus* fed more heavily on Trichoptera and internal organs of large insects. *Myotis californicus* fed on Lepidoptera at a rate similar to that of *M. yumanensis,* but also greatly on Tipulidae, little on Isoptera, and did not consume internal organs of large insects. Some of these differences may reflect differences in availability of insects at the time and place where the bats fed, but others seem definitely to reflect selectivity of prey among the bats and/or adaptability towards capture of certain groups of prey. Consumption of almost 100 percent lepidopterans by *Plecotus,* and the complete absence of this food in *Antrozous,* certainly reflects more than simple feeding on the basis of availability.

*Antrozous pallidus* is known to take food items regularly from the ground, but other bat species also quite often take non-flying foods (Whitaker, 1972). Araneida, for example, are often taken by bats and in our sample of *Myotis evotis* and *M. californicus,* this food approached 10 percent of the diet. How Araneida are obtained is not known, but it is likely they are taken in or around the roosting areas of the bats. Possibly they are taken from the ground, foliage, or while suspended from their webbing.

## Conclusions

Examination of the data suggests that, instead of competition, there is inter-specific partitioning of the food supply. Bats feed at different times, at different heights above the ground, in different areas of a given habitat, and tend to select for certain groups

of species within the insect-arachnid fauna. These behavioral differences allow maximum efficiency in bat utilization of both the available habitat and the source of food.

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# Reproduction of the California Red-Backed Vole in Western Oregon

**Abstract**

Two hundred and sixty *Clethrionomys californicus* specimens were collected in western Oregon from 1952 to 1965. The sex ratio of 258 animals was 49 percent males. The range of shortest body lengths for fecund animals was 90 to 99 mm for males and 80 to 89 mm for females. Males were in breeding condition from February to October and females from April to November, based on the combined years. Average number per set of corpora lutea was 2.86, placental scars 2.91, and embryos 2.63. Seventeen percent of the lactating females had postpartum pregnancies and the calculated minimum number of litters per year was 3.1.

California red-backed voles *(Clethrionomys californicus)* occur from the Columbia River southward along the coast to Sonoma County, California. They frequent the deep woods in the Transition and Canadian life zones from the upper western edge of the ponderosa pine *(Pinus ponderosa)* type on the eastern slope of the Cascade Mountains to the Pacific Ocean (Bailey, 1936; Ingles, 1965; and Maser and Storm, 1970).

During the course of a forest-wildlife ecological study in Oregon from 1952 to 1967, 260 red-backed voles were collected and 243 were given post-mortem examinations. Although the samples were not as well distributed throughout the year nor as large as desired, considerable new knowledge about California red-backed voles was obtained.

## Location and Description of Study Area

Voles were collected on the Half Pint area, Lakes Ranger District, Mt. Hood National Forest, Clackamas Co., and on the H. J. Andrews Experimental Forest and vicinity, Blue River Ranger District, Willamette National Forest, Lane and Linn counties, Oregon. Both areas are on the west slope of the Cascade Mountains in the northern half of the state. The undulating terrain is composed of irregular benches alternating with steep slopes and the soils are generally a porous, clay loam. Precipitation ranges from about 200 to 320 cm per year, and occurs mostly in winter.

Most of the voles were caught in old-growth timber, primarily Douglas-fir *(Pseudotsuga menziesii)* with smaller amounts of western hemlock *(Tsuga heterophylla)* and western redcedar *(Thuja plicata)*. Scattered throughout the forest were western yew *(Taxus brevifolia)*, vine maple *(Acer circinatum)*, big-leaf maple *(Acer macrophyllum)*, and flowering dogwood *(Cornus nuttallii)*. Ground cover in the mature forest was variable but was largely shrubby and often of salal *(Gaultheria shallon)*, sword fern *(Polystichum munitum)*, Oregon grape *(Berberis nervosa)*, rhododendron *(Rhododendron macrophyllum)*, twin-flower *(Linnaea borealis)*, and gold-thread *(Coptis laciniata)*. Grasses and sedges formed only a small percentage of the vegetation.

### Methods

Red-backed voles were caught in ordinary household and Museum Special kill-traps set on line transects. Some specimens came from animals which succumbed in Sherman live-traps set on a grid pattern and on line transects. Most of the trapping in the mature forest was at elevations ranging from about 396 to 1,219 m and on a spring and fall schedule.

Measurements and other external information, such as condition of genital organs, were obtained before the specimens were dissected. A small number of slides were made, primarily from testes, and examined for sperm abundance. Large (8.0 mm and longer) pink and turgid testes, and cauda epididymides tubules visible to the unaided eye were considered evidence of male fecundity. The size and condition of the seminal vesicles were also evaluated. Females were considered fecund if they had embryos or were lactating; perforate vulvas, recent ovulation, and general size and condition of the sex organs were also considered in the evaluation. Voles having evidence of present or past sexual activity were classed as adults.

Scientific names of mammals and plants used in this article follow Bailey (1936) and Hitchcock *et al.* (1955-69), respectively.

### Results and Discussion

Yearly *Clethrionomys* samples were generally small and too variable to be treated separately so the data were combined by months for the entire period. Even so, the March, April, and August samples are very small.

*Sex Ratios.* Males made up 49 percent (126) of the 258 animals examined. There was no significant difference (t test, $P < 0.05$) in the number of males and females captured. The males formed the bulk of the small samples in February, March, and August, and were equal to or only slightly less abundant than females in May, June, July, September, October, and November. Females dominated the samples in January, April, and December. The sex ratio of 97 *Clethrionomys californicus* captured during the early part of this study was 56 percent males (Gashwiler, 1959), a greater percentage than for the larger sample. Of 15 California red-backed voles captured in Oregon from 1893 to 1937 by several collectors (Macnab and Dirks, 1941), 40 percent (6) were males. However, this sample is a very small one and the results are probably not representative.

*Reproductive Periods and Fecundity Rates.* The male breeding season lasted nine months; it began in February, and most males were in breeding condition from March to September (Table I). Only a few males were fecund in October. The females had a shorter (8 months) breeding season which started in April, two months later than the males. The sample of females, however, was very small from January to March, and fecund females could easily have been missed. High fecundity rates of females prevailed until September when a moderate decline occurred. This decline continued gradually until November when no females were found in breeding condition. The weighted fecundity percentage (each monthly percentage divided by the total sum of all monthly percentages) for both sexes was relatively uniform from March to September (Table 1) which suggests a continuous productivity period and numerous litters per season for each female. I reported earlier that red-backed voles in Oregon are in breeding condition from April through November on the basis of a smaller sample (Gashwiler, 1959).

In the present study both sexes of red-backed voles were found reproductively active

TABLE 1. Number and percentage of adult fecund red-backed voles by month, sex, total, and weighted values.[a]

| Months | Males | | | Females | | | Total | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | No. coll. | No. fecund | % fecund | No. coll. | No. fecund | % fecund | No. coll. | No. fecund | % fecund | Weighted % fecund |
| Jan. | — | — | — | 2 | 0 | 0 | 2 | 0 | 0 | 0.0 |
| Feb. | 8 | 2 | 25 | 1 | 0 | 0 | 9 | 2 | 22 | 3.0 |
| Mar. | 4 | 4 | 100 | 1 | 0 | 0 | 5 | 4 | 80 | 10.9 |
| April | 2 | 2 | 100 | 4 | 4 | 100 | 6 | 6 | 100 | 13.6 |
| May | 19 | 19 | 100 | 20 | 19 | 95 | 39 | 38 | 97 | 13.2 |
| June | 6 | 6 | 100 | 7 | 7 | 100 | 13 | 13 | 100 | 13.6 |
| July | 1 | 1 | 100 | 2 | 2 | 100 | 3 | 3 | 100 | 13.6 |
| Aug. | 6 | 6 | 100 | 3 | 3 | 100 | 9 | 9 | 100 | 13.6 |
| Sept. | 16 | 14 | 88 | 24 | 19 | 79 | 40 | 33 | 83 | 11.3 |
| Oct. | 37 | 8 | 22 | 44 | 27 | 61 | 81 | 35 | 43 | 5.8 |
| Nov. | 12 | 0 | 0 | 17 | 3 | 18 | 29 | 3 | 10 | 1.4 |
| Dec. | 4 | 0 | 0 | 3 | 0 | 0 | 7 | 0 | 0 | 0.0 |
| Total and avg. | 115 | 62 | 54 | 128 | 84 | 66 | 243 | 146 | 60 | 100.0 |

[a] See text for definition of fecundity for each sex, and weighting procedure.

from February through November, a 10-month period. Since this sample is a composite of many years, it probably includes years in which reproduction began early as well as late, and may represent a longer breeding period than occurs in any one year.

Early born *Clethrionomys* probably matured and became part of the breeding population of the year. The red-backed voles were grouped into 10mm body length classes, *i.e.,* 80 to 89 mm, etc. The smallest male red-backed voles considered fecund were in the 90 to 99 mm body length class. Smaller males, in the 80 to 89 mm class, were not captured until September, and were considered late young of the year. The smallest mature females were in the 80 to 89 mm body length class. The data suggest that females reach sexual maturity at a shorter body length (younger age) than males.

*Litter size.* Averages and ranges of litter size as determined by corpora lutea, placental scars, and embryo sets for California red-backed voles are given in Table 2 by reproductive stage. The average number of placental scars was slightly greater than the number of corpora lutea (2.91 vs. 2.86); this figure may be the result of sample differences or formation of some multiple zygotes from single follicles. Beer *et al.* (1957) thought multiple zygotes might exist among cricetid rodents in Minnesota. However, the hypothesis of sample differences seems more likely for my data since the average number of embryos per female was 2.63 as compared to 2.86 corpora lutea. Maser and Storm (1970) reported a range of one to six young (embryos by inference) per litter with

TABLE 2. Number of corpora lutea, placental scars, and embryos of red-backed voles.

| Reproductive stage | No. of sets | Total No. of entities | Ave. Sets and SE | Mode of sets | Range of sets |
|---|---|---|---|---|---|
| Corpora lutea | 81 | 232 | 2.86 ± 0.13 | 3 | 2-7 |
| Placental scars | 57 | 166 | 2.91 ± 0.12 | 2 | 1-7 |
| Embryos | 24 | 63 | 2.63 ± 0.02 | 3 | 1-4 |

most litters ranging from two to four for the red-backed vole in Oregon. This is a greater spread in range than was found in the present study, but the mode may have been the same. Larger samples would probably bring the two sets of data into closer agreement.

*Postpartum Pregnancies.* Four of the 24 pregnant red-backed voles were also lactating; thus at least 17 percent of the females had bred soon after parturition. Palmer (1954) reported a female that bred within 12 hours after giving birth. Seventeen percent is probably a minimum figure, since early stages of pregnancy could easily be overlooked. The ability to sustain reproductive processes over a possible eight-month or longer period and capability to produce postpartum pregnancies gives the red-backed vole great breeding potential. On the other hand, the relatively small average litter size of 2.6 young tends to restrict this potential.

*Calculated Number of Litters Per Year.* Number of litters per year was calculated by the method used by Gashwiler (1972). The monthly percentage of pregnant females was summed for the year and multiplied by the total number of days in the months with pregnancies. This product was divided by 18, the average number of days in the gestation period (Palmer, 1954). The resulting figure was then divided by the number of months in which pregnancies were found to give the estimated number of litters per year. The California red-backed voles averaged 3.1 litters per year. However, this figure is considered low since the samples in July and August were only one and two females and no pregnancies were found. If the June percentage of pregnancy is assumed for July and the September percentage for August, a very rough estimate of 4.6 litters per year is obtained. Obviously, such an estimate should be used very cautiously since the July and August pregnancy percentages are unknown.

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# Plants and Soil of a Sagebrush Community on the Hanford Reservation[1]

**Abstract**

This study defines a sagebrush/cheatgrass community on the Hanford Reservation, Benton County, Washington. Twenty-seven herbaceous species were observed. The average understory cover was 38 percent. Cheatgrass, an annual grass, was the dominant species and provided 18 percent of the herbaceous cover. Sagebrush was the conspicuous shrub, providing 15 to 20 percent of the total cover. Biomass production of the herbaceous species was approximately 40 g/m$^2$. Soil analysis and the mineral composition of the vegetation were measured and evaluated.

## Introduction

The Hanford Reservation, Benton County, Washington, lies within the boundaries of the sagebrush vegetation zone (Daubenmire, 1970). However, the land on the Hanford Reservation located west of the Columbia River can be mapped as three different vegetation types (Fig. 1). The sagebrush-bitterbrush/cheatgrass type occupies a triangular shaped area with its apex near the old Hanford townsite and extends southward to the Horn Rapids bend of the Yakima River. The sagebrush/bluebunch wheatgrass vegetation type is confined to the Rattlesnake Hills at elevations of above 900 ft. The vegetation between these two is designated as the sagebrush/cheatgrass vegetation type. This latter type occupies much of the area of Hanford Reservation. It differs from the sagebrush/bitterbrush by lacking bitterbrush and the absence of bluebunch wheatgrass distinguishes it from the sagebrush/bluebunch wheatgrass type. This paper describes the sagebrush/cheatgrass vegetation type that is not regarded in pristine condition by Daubenmire because it contains large amounts of cheatgrass *(Bromus tectorum),* an alien plant characteristic of man-induced disturbances, such as grazing by domestic cattle and sheep. Nevertheless, this vegetation type is important on the Hanford Reservation because nuclear energy facilities are a major long-term use of some of the land.

The purpose of this investigation was to describe the vegetation and the surface soil of a sagebrush/cheatgrass community located near the chemical separation facilities known as the 200 East and 200 West areas but well inside the boundaries of access control zones. The area has been protected from grazing livestock since 1943.

## Methods Employed

The experimental design consisted of two stands designated as Site I and Site II located centrally in the sagebrush/cheatgrass vegetation type at an elevation of 700 ft above sea level (Fig. 2). Each site contained two replicates consisting of four 50-mm tran-

[1] Work performed for the Atlantic Richfield Hanford Company under United States Energy Research and Development Administration contract E(45-1)-2130.

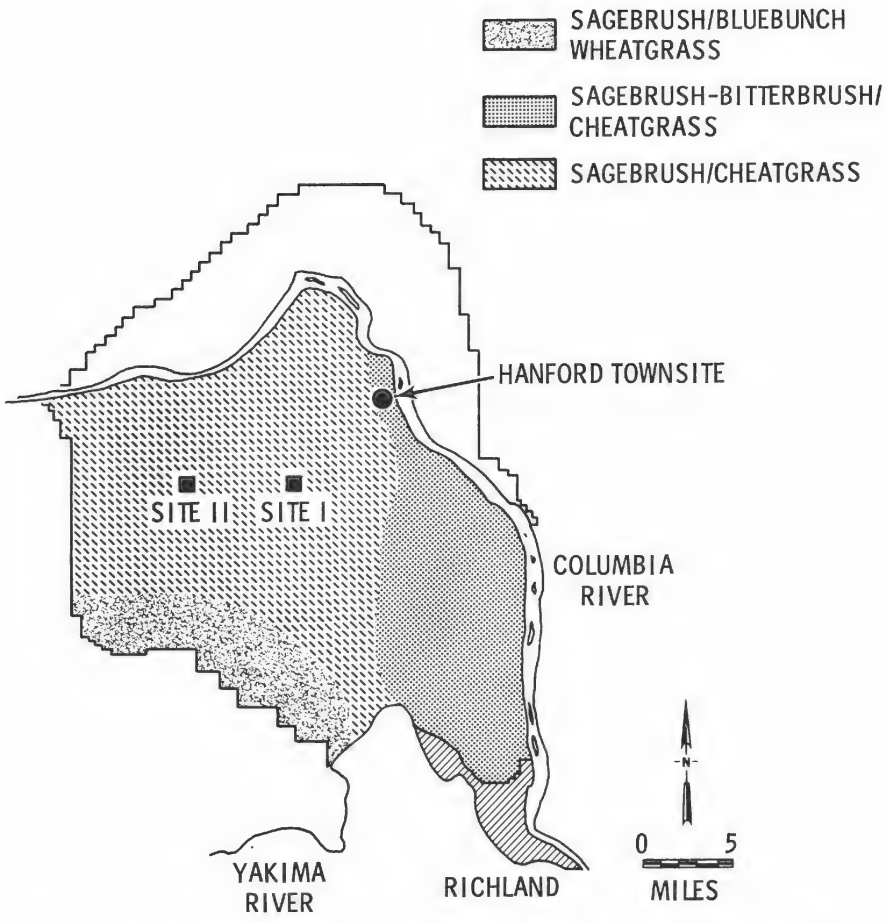


Figure 1. Geographic extent of three major vegetation types and the location of study sites I and II on the Hanford Reservation.

sects arranged parallel to each other and systematically spaced at 30-m intervals. Shrub density was estimated by counting all individuals rooted inside a 10 x 50 m (500 $m^2$) study plot in each replicated area. Each shrub was measured for long and short diameters and also extreme shoot height from ground level. Canopy cover provided by herbaceous taxa was measured by reading fifty 2 x 5 dm plot frames systematically spaced at one-meter intervals on each line transect. In all, 400 plots were read at each site. Cover for each taxon was ocularly estimated using a modified method of canopy cover analysis developed by Daubenmire (1959). Modified classification numbers were 1 $<$ 5 percent, 2 $=$ 5-15 percent, 3 $=$ 15-25 percent, 4 $=$ 25-50 percent, 5 $=$ 50-75 percent, and 6 $=$ 75-100 percent.

Aboveground biomass was estimated by hand-clipping herbaceous plants located within a 0.5 $m^2$ circular plot. Four plots were systematically spaced along each line

transect. Live material representing the current year's growth was hand separated from dead plant material. All material was oven-dried at 60°C and weighed. The plant material was ground in a Wiley mill to pass through a 1 mm screen mesh and chemically analyzed for macro- and micronutrient content by the U.S. Testing Co., Richland, Washington.

Belowground biomass was obtained by drilling a single hole into the soil profile located within the clipped circular plots. A total of 16 holes were drilled into the soil profile at Site I. Each soil increment one decimeter deep was washed in running tap water and the roots retained on a fine mesh screen. Roots were floated to eliminate large soil particles. All roots were oven-dried, ashed at 500°C over a 24-hour period, and expressed as ash-free weight.

Four soil cores were sampled at random at each site for textural and chemical analyses. All field sampling was conducted between April 24 and May 6, 1974.

#### Results

*Botanical Measurement:* A total of 27 herbaceous species (taxa) were observed on 800 plots (Tables 1 and 2); 20 taxa occurred on each site. Annual grasses and forbs dominated the canopy cover while perennial grasses and forbs provided small amounts of cover. Average canopy cover was 37 percent for Site I and 39 percent for Site II (Tables 1 and 2). More than 60 percent of the ground area did not support herbs and was either bare or supported a thin crust of algae, mosses, and lichens. Clearly, the most important herb was cheatgrass. It alone provided almost half of the herbaceous cover. Tansy mustard *(Descurainia pinnata)* was the most important annual forb in terms of canopy-cover.

Russian thistle *(Salsola kali)* was more important to canopy-cover than shown in Table 1 because of the season of the year in which the observations were recorded. Russian thistle can grow throughout the summer and flowers in late summer. It can sometimes attain sizes as large as sagebrush shrubs.

Shrubs are the conspicuous plants of the plant community; however, only three species were present. These were sagebrush *(Artemisia tridentata)* and two species of rabbitbrush *(Chrysothamnus nauseosus* and *C. viscidiflorus). Artemisia* canopy cover ranged between 15 and 26 percent (Table 3) and *Chrysothamnus* between 0 and 3 percent. The average number of shrubs was 243 $\pm$ 98/1000 $m^2$ (Table 3). Site I suported 376 and Site II 110 shrubs. Site I with the greatest shrub density had the shortest statured plants with small canopy areas. At either site, less canopy cover was provided by shrubs than by associated herbs.

The live biomass (net primary production) of herbs by species is shown in Table 4. The data were obtained only for Site I, but results are not expected to be much different at Site II. The total aboveground biomass, excluding shrubs, was measured at 40 $g/m^2$ dry weight of which almost half, 18 grams, was provided by cheatgrass. No estimates of shrub weight were obtained in this study.

Total root mass, which includes roots from shrubs in the upper meter of soil profile, was estimated at 368 $g/m^2$. More than half was located in the upper 3 dm of soil profile (Fig. 3).

*Mineral Content of Plants:* The concentrations of macronutrients in the tissues of important grass and forb species are shown in Table 5. On the average, micro- and ma-

TABLE 1. Canopy cover provided by herbaceous taxa at study site I.

| Taxa | $T_1$[1] | $T_2$ | $T_3$ | $T_4$ | Ave[1] Rep 1 $\bar{X}$ | $T_1$ | $T_2$ | $T_3$ | $T_4$ | Ave Rep 2 $\bar{X}$ | Ave Rep 1&2 $\bar{X} \pm$ SE. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Annual Grasses* | | | | | | | | | | | |
| *Bromus tectorum* | 13.0 | 15.7 | 25.6 | 16.7 | 17.8 | 10.3 | 9.1 | 12.4 | 19.4 | 12.8 | 15.3 ± 0.9 |
| *Festuca octoflora* | 1.9 | 2.0 | 3.1 | 2.5 | 2.4 | 6.0 | 6.2 | 6.3 | 4.1 | 5.7 | 4.0 ± 0.7 |
| *Annual Forbs* | | | | | | | | | | | |
| *Descurainia pinnata* | 7.5 | 9.1 | 10.9 | 11.7 | 9.8 | 9.1 | 4.8 | 8.4 | 2.9 | 6.3 | 8.0 ± 1.0 |
| *Microsteris gracilis* | 1.5 | 4.9 | 3.1 | 2.7 | 3.1 | 3.7 | 2.5 | 5.4 | 2.0 | 3.4 | 3.2 ± 0.5 |
| *Cryptantha circumscissa* | 2.1 | 1.7 | 1.4 | 1.8 | 1.7 | 0.9 | 2.5 | 1.7 | 2.3 | 1.9 | 1.8 ± 0.2 |
| *Cryptantha pterocarya* | 1.2 | 0.05 | 0.8 | 0.5 | 0.6 | 0.9 | 0.5 | 0.5 | 0 | 0.5 | 0.6 ± 0.1 |
| *Phacelia linearis* | 0.05 | 0 | 0 | 0 | 0.01 | 0.2 | 0.8 | 0.7 | 0.05 | 0.5 | 0.02 ± 0.1 |
| *Erysimum asperum* | 1.6 | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0.2 ± 0.2 |
| *Salsola kali* | 0.05 | 0.3 | 0.1 | 0.1 | 0.1 | 0.05 | 0.5 | 0 | 0 | 0.1 | 0.1 ± 0.1 |
| *Sisymbrium altissimum* | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 | 0 | 0 | 0.05 | 0.03 ± 0.03 |
| *Amsinckia lycopsoides* | 0.35 | 0.1 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0.05 ± 0.04 |
| *Perennial Grasses* | | | | | | | | | | | |
| *Poa sandbergii* | 4.6 | 1.8 | 1.6 | 2.7 | 2.7 | 1.0 | 1.0 | 1.0 | 0.3 | 0.8 | 1.7 ± 0.5 |
| *Perennial Forbs* | | | | | | | | | | | |
| *Phlox longiflora* | 0.2 | 0 | 0 | 0 | 0.1 | 1.8 | 1.2 | 2.2 | 0 | 1.3 | 0.7 ± 0.3 |
| *Cymopterus terebinthinus* | 0.05 | 0 | 0 | 0 | 0.01 | 0.8 | 1.2 | 0 | 0 | 0.5 | 0.3 ± 0.2 |
| *Eriogonum* spp. | 0.5 | 0 | 0 | 0.1 | 0.2 | 0.3 | 1.3 | 0.2 | 0.6 | 0.6 | 0.4 ± 0.2 |
| *Balsamorhiza careyana* | 1.0 | 0 | 0 | 0 | 0.3 | 0.2 | 0 | 0 | 0 | 0.05 | 0.2 ± 0.1 |
| *Brodiaea douglasii* | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.1 | 0.05 | 0 | 0.1 | 0.03 ± 0.02 |
| *Commandra pallida* | 0 | 0 | 0 | 0 | 0 | 0.2 | 0.05 | 0 | 0 | 0.1 | 0.03 ± 0.02 |
| *Oenothera pallida* | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.05 | 0 | 0 | 0.04 | 0.02 ± 0.01 |
| *Calochortus macrocarpus* | 0 | 0 | 0 | 0 | 0 | 0.05 | 0.1 | 0.15 | 0 | 0.1 | 0.04 ± 0.02 |
| Total Cover | 35.7 | 35.6 | 46.6 | 38.7 | 39.2 | 35.9 | 31.9 | 39.0 | 31.6 | 34.8 | 36.9 |
| Number of Species — 20 | | | | | | | | | | | |

[1] T = Transects, Rep = Replicate

TABLE 2. Canopy coverage provided by herbaceous taxa at study site II.

| Taxa | $T_1$[1] | $T_2$ | $T_3$ | $T_4$ | Ave[1] Rep 1 $\bar{X}$ | $T_1$ | $T_2$ | $T_3$ | $T_4$ | Ave Rep 2 $\bar{X}$ | Ave Rep 1&2 $\bar{X} \pm$ SE. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Annual Grasses* | | | | | | | | | | | |
| *Bromus tectorum* | 20.8 | 24.2 | 20.8 | 21.9 | 21.9 | 26.2 | 27.7 | 15.0 | 18.2 | 21.8 | 21.9 ± 1.1 |
| *Festuca octoflora* | 2.8 | 2.3 | 6.1 | 2.9 | 3.5 | 0.9 | 0.7 | 3.0 | 1.4 | 1.5 | 2.4 ± 0.6 |
| *Annual Forbs* | | | | | | | | | | | |
| *Descurainia pinnata* | 2.2 | 2.1 | 1.2 | 2.7 | 2.0 | 9.3 | 4.1 | 1.9 | 3.6 | 4.7 | 3.4 ± 0.9 |
| *Cryptantha circumscissa* | 2.1 | 1.9 | 1.6 | 10.8 | 4.1 | 1.0 | 1.5 | 1.7 | 1.8 | 1.5 | 2.8 ± 1.2 |
| *Sisymbrium altissimum* | 0.3 | 0 | 0.1 | 0 | 0.1 | 3.5 | 5.7 | 1.5 | 0.2 | 2.5 | 1.4 ± 0.8 |
| *Salsola kali* | 0.1 | 0 | 0 | 0 | 0.02 | 0.02 | 0.2 | 0.6 | 0.4 | 0.35 | 0.2 ± 0.1 |
| *Cryptantha pterocarya* | 0.8 | 0.3 | 1.1 | 3.3 | 1.4 | 0.4 | 0 | 0 | 0 | 0.1 | 0.7 ± 0.4 |
| *Microsteris gracilis* | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.1 | 0 | 0 | 0.05 | 0.03 ± 0.02 |
| *Perennial Grasses* | | | | | | | | | | | |
| *Stipa comata* | 13.0 | 2.7 | 3.6 | 1.4 | 7.9 | 0 | 0 | 0 | 0 | 0 | 2.0 ± 1.6 |
| *Agropyron dasytachyum* | 0 | 0 | 0 | 0 | 0 | 0.4 | 5.1 | 0 | 0 | 0 | 0.7 ± 0.6 |
| *Poa canbyi* | 1.5 | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0.2 ± 0.2 |
| *Poa sandbergii* | 0 | 0 | 1.8 | 0.3 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0.3 ±00.2 |
| *Sitanion hystrix* | 0 | 0 | 0 | 0 | 0 | 0.05 | 0 | 0 | 0 | 0 | <0.1 |
| *Perennial Forbs* | | | | | | | | | | | |
| *Cymopterus terebinthinus* | 1.2 | 0 | 7.9 | 7.8 | 4.2 | 0 | 0 | 0 | 0 | 0 | 2.0 ± 1.3 |
| *Erigeron* sp. | 0.1 | 0.9 | 0.4 | 0.1 | 0.4 | 0.1 | 0.2 | 0.1 | 0.1 | 0.1 | 0.3 ± 0.1 |
| *Aster canescens* | 0.3 | 0 | 0 | 0 | 0.08 | 0.4 | 0.4 | 0.2 | 0.7 | 0.4 | 0.3 ± 0.1 |
| *Oenothera pallida* | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.03 | 0.01 ± 0.01 |
| *Calochortus macrocarpus* | 0.1 | 0 | 0 | 0 | 0.03 | 0 | 0 | 0 | 0 | 0 | 0.01 ± 0.01 |
| *Lupinus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.0 | 0 | 0.5 | 0.3 ± 0.3 |
| *Phlox longifolia* | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | <0.1 |
| Total Cover % | 45.4 | 34.4 | 44.7 | 51.2 | 46.2 | 42.6 | 45.7 | 26.0 | 26.4 | 33.5 | 38.9 ± |
| Number of taxa — 20 | | | | | | | | | | | |

[1] T = Transect, Rep = Replicate

TABLE 3. Average shrub measurements of canopy cover, height, and area (L x W) and density for Sites I and II.

| Taxa | Site I Rep 1[1] | Site I Rep 2 | Site I $\bar{X}$ | Site II Rep 1 | Site II Rep 2 | Site II $\bar{X}$ |
|---|---|---|---|---|---|---|
| | | | Canopy Coverage (%) | | | |
| *Artemisia* | 26.3 | 25.4 | 25.8 | 21.2 | 15.3 | 18.2 |
| SE | ±5.7 | ±5.7 | ±4.3 | ±3.5 | ±3.8 | ±2.7 |
| Chrysothamnus | 0 | 0.8 | 0.4 | 0.5 | 2.7 | 1.6 |
| | | ±0.8 | ±0.4 | ±0.5 | ±1.3 | ±0.7 |
| | | | Height (cm) | | | |
| *Artemisia* | 102 | 78 | 85 | 95 | 116 | 104 |
| SE | ±3 | ±2 | ±1 | ±5 | ±4 | ±4 |
| | | | Area (L x W) $cm^2$ | | | |
| *Artemisia* | 14200 | 6720 | 10450 | 23100 | 25880 | 24350 |
| SE | ±960 | ±360 | ±420 | ±2390 | ±2630 | ±1760 |
| | | | Number of Shrubs Per 1000 $m^2$ | | | |
| *Artemisia* | 226 | 518 | 372 | 94 | 76 | 84 |
| *Chrysothamnus* | 0 | 8 | 4 | 14 | 36 | 26 |
| TOTAL | 226 | 526 | 376 | 108 | 112 | 110 |

[1] Rep = Replicate

TABLE 4. Aboveground live biomass $g/m^2$ of herbaceous plant taxa (mean ± SE) or replicates at Site I on the 200-Area Plateau, Hanford Reservation, 1974.

| Taxa | Rep 1[1] | Rep 2 | Mean |
|---|---|---|---|
| Annual grasses | | | |
| *Bromus tectorum* | 19 ± 4.6 | 17 ± 3.7 | 18 |
| *Festuca octoflora* | 3.0 ± 1.1 | 10 ± 2.3 | 6.6 |
| Total | 22 | 27 | 25 |
| Perennial grasses | | | |
| *Agropyron spicatum* | 0 | 3.6 ± 3.6 | 1.8 |
| *Sitanion hystrix* | 3.6 ± 3.6 | 0 | 1.8 |
| *Poa sandbergii* | 1.3 ± 0.5 | 0.8 ± 0.4 | 1.0 |
| Total | 4.9 | 3.4 | 3.8 |
| Perennial forbs | | | |
| *Erigeron filifolius* | 0.01 ± 0.01 | 0.01 ± 0.01 | 0.01 |
| *Brodiaea douglasii* | 0 | 0.01 ± 0.01 | |
| *Calochortus macrocarpus* | 0 | 0.94 | 0.48 |
| Total | 0.01 | 0.96 | 0.49 |
| Annual forbs | | | |
| *Descurainia pinnata* | 6.4 ± 1.6 | 5.1 ± 1.2 | 5.7 |
| *Microsteris gracilis* | 2.0 ± 1.4 | 2.8 ± 1.1 | 2.4 |
| *Cryptantha circumscissa* | 2.7 ± 1.4 | 1.2 ± 0.5 | 2.0 |
| *Phlox longifolia* | 0 | 0.76 ± 0.76 | 0.38 |
| *Cryptantha pterocarya* | 0.41 ± 0.26 | 0.05 ± 0.03 | 0.23 |
| *Phacelia linearis* | 0.01 ± 0.01 | 0.30 ± 0.15 | 0.15 |
| *Amsinckia lycopsoides* | 0.05 ± 0.05 | 0 | 0.03 |
| *Salsola kali* | 0.10 ± 0.06 | 0.06 ± 0.04 | 0.08 |
| *Sisymbrium altissimum* | 0 | 0.20 ± 0.02 | 0.10 |
| Total | 12 | 10 | 11 |
| Total herbs $g/m^2$ | 39 ± 6.4 | 41 ± 5.9 | 40 ± 4.3 |

[1] Rep = Replicate

cronutrient content was greater in forbs than in grasses. This finding is particularly evident in potassium and calcium contents. Nitrogen content was similar in forb and grass tissues.

Figure 2. Sagebrush/cheatgrass vegetation type representative of the study area on the Hanford Reservation.

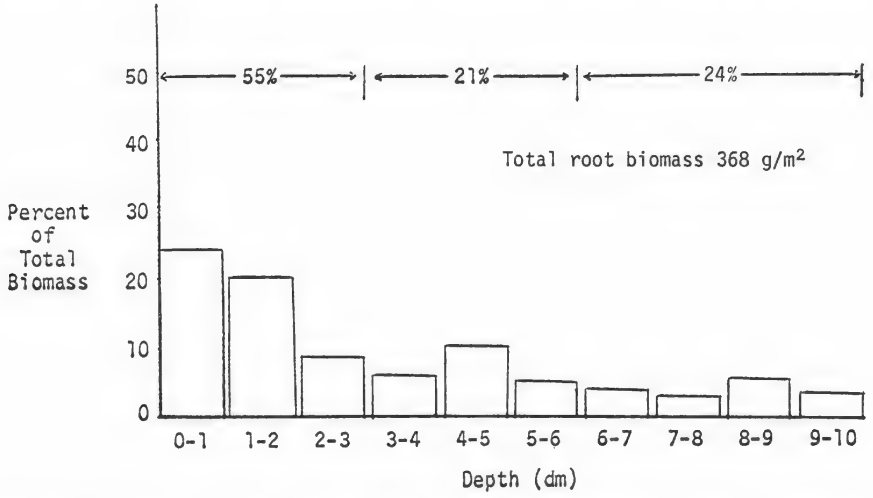


Figure 3. Distribution of roots (live and dead) in the upper meter of soil profile in a sagebrush-cheatgrass community at Site I.

TABLE 5. Mineral nutrient content of herbaceous plant taxa from Site I.

| Taxa | Macronutrients (% Dry Wt.) | | | | | | | Micronutrients (% Dry Wt.) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | P | K | Ca | Mg | Na | S | Fe | Mn | B | Cu | Zn |
| Grasses | | | | | | | | | | | | |
| *Bromus tectorum* | 0.92 | 0.17 | 1.17 | 0.43 | 0.16 | 0.03 | 0.10 | 0.04 | 0.004 | 0.001 | 0.0003 | 0.001 |
| *Festuca octoflora* | 0.93 | 0.14 | 0.65 | 0.40 | 0.13 | 0.02 | 0.14 | 0.04 | 0.006 | 0.002 | 0.0002 | 0.002 |
| *Poa sandbergii* | 1.17 | 0.18 | 0.75 | 0.40 | 0.12 | 0.05 | 0.13 | 0.05 | 0.004 | 0.002 | 0.0003 | 0.001 |
| Average | 1.00 | 0.16 | 0.86 | 0.41 | 0.14 | 0.03 | 0.02 | 0.04 | 0.005 | 0.002 | 0.0003 | 0.001 |
| Forbs | | | | | | | | | | | | |
| *Descurainia pinnata* | 1.34 | 0.29 | 1.13 | 1.16 | 0.26 | 0.04 | 0.31 | 0.03 | 0.002 | 0.003 | 0.0005 | 0.002 |
| *Microsteris gracilis* | 0.71 | 0.19 | 0.88 | 1.49 | 0.27 | 0.08 | 0.14 | 0.21 | 0.006 | 0.003 | 0.0004 | 0.002 |
| *Cryptantha circumscissa* | 1.13 | 0.38 | 1.08 | 5.40 | 0.41 | 0.06 | 0.13 | 0.13 | 0.007 | 0.006 | 0.0004 | 0.002 |
| *Cryptantha pterocarya* | 1.09 | 0.14 | 2.14 | 1.73 | 0.17 | 0.05 | 0.12 | 0.06 | 0.005 | 0.005 | 0.0003 | 0.001 |
| Average | 1.07 | 0.25 | 1.31 | 2.44 | 0.28 | 0.06 | 0.17 | 0.11 | 0.005 | 0.004 | 0.0004 | 0.002 |

*Soil Properties:* Soil texture is important to plant growth because it determines to a large extent the water-holding capacity of a given volume of soil and also its cation exchange capacity. Soils were similar in texture, *i.e.,* sandy loams at both sites (Table 6). Sand dominated the three textural classes followed by silt and clay. Clay-sized particles were scarce, making up only 1 percent of the texture size classes. These data imply that the moisture-holding capacity and cation exchange of the soil profile are low. Also, these sandy soils are subject to serious wind erosion when disturbed (Hinds and Sauer, 1974).

The pH values of surface soils are alkaline, and alkalinity increases with profile depth (Table 6). Soluble salts are low, indicating that salinity (excess salts) is not a hinderance to plant growth, at least in the upper soil. Organic matter is low, indicative of low soil nitrogen levels.

**Discussion**

The sagebrush/cheatgrass community described is probably very much like the community that existed prior to 1943 when the Hanford Reservation was established. The major vegetational change has been the incorporation of weeds of European origin into the plant community. The most successful of these European weeds is cheatgrass, and it has probably been a member of the plant community for a century. This grass was an important plant on Benton County rangelands a half century ago (St. John and Jones, 1928). Cheatgrass is so well adapted to the climatic and soil conditions of the Hanford Reservation that it is prudent to consider the species as an integral part of the flora and to make use of its pioneering aggressiveness in revegetating disturbed land.

The number of plant species in the study area was less when compared to other kinds of natural plant communities in eastern Washington and the annual production of dry land matter is also less (Daubenmire, 1970; Rickard, 1975; Cline and Rickard, 1973). The low species diversity is attributed to the generally level terrain, *i.e.,* habitat homogeneity and the low annual precipitation which over a 30-year period has averaged only 6.3 inches. Sandy soils having a low water-holding capacity and available nutrients will influence diversity.

Sagebrush, the important shrub community, is not palatable to livestock. The most important livestock forage species, in terms of palatability and abundance, is *Bromus*

TABLE 6. Average chemical and physical properties of soil from Sites I and II.

| | Soil Depth (dm) | | | | | | |
|---|---|---|---|---|---|---|---|
| | 0-1 | 1-2 | 2-3 | 3-4 | 4-5 | 5-6 | Avg |
| Texture | | | | | | | |
| % Sand | 59 | 62 | 67 | 63 | 57 | 57 | 61 |
| % Silt | 40 | 37 | 32 | 36 | 42 | 42 | 38 |
| % Clay | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Organic Matter % | 0.68 | 0.45 | 0.35 | 0.43 | 0.43 | 0.50 | 0.47 |
| Elec. Cond. mmhos/cm | 0.25 | 0.20 | 0.24 | 0.29 | 0.21 | 0.30 | 0.25 |
| pH | 7.5 | 7.6 | 7.7 | 7.9 | 7.9 | 8.1 | 7.8 |

*tectorum.* However, the grazing season is short. If one-half of the herbaceous production could be ingested by livestock, an intake of about 200 kg of dry matter per ha (200 lbs per acre) is potentially available as livestock forage. The conclusion is that species diversity and net productivity and livestock grazing capacity is inherently lower here than other steppe plant communities of eastern Washington.

In the absence of livestock, the most important mammalian herbivore on the study site is the black-tailed hare *(Lepus californicus).* A study of the dietary habits of black-tailed hares on the Hanford Reservation (Uresk *et al.,* 1975) indicates that cheatgrass was not eaten by hares; shrubs were sparingly eaten, with rabbitbrush being taken in preference to sagebrush. Perennial forbs, such as yarrow *(Achillea millefolium)* and turpentine cymopterus *(Cymopterus terebinthinus),* plants sparsely represented in the community, were the preferred hare foods.

Two kinds of environmental stresses can be expected to be imposed on this community in the future. These are: (1) fire and (2) mechanical soil disturbances. Fire can be naturally induced by lightning or ignited by man. Burning destroys sagebrush plants but perennial grasses and forbs generally survive and send out new shoots. At least some seeds of annuals survive the burning and provide a crop during the year of post-burning. Recolonization of the burned areas may also be accomplished by seed imported from surrounding surviving vegetation.

Mechanical disturbances, such as imposed in the construction activities of this area, effectively destroy all existing vegetation. Russian thistle is one of the most aggressive of the early invaders and may dominate in the first year, but thereafter cheatgrass assumes dominance and it resists invasion by native plants and Salsola. Daubenmire (1975) describes cheatgrass as dominating the vegetation of an abandoned agricultural field for 52 years with little invasion by native perennials although nearby seed sources were available. Of the shrubby species, rabbitbrush is more aggressive than sagebrush in terms of invading disturbed soils.

Unless there are major changes in land use, such as irrigated agriculture, livestock grazing, or new construction activities associated with Hanford Reservation industrial activities, the plant community described here is expected to maintain essentially the same species composition and productivity as described herein in the forseeable future, *i.e.,* 20-30 years. Wildfire is the most likely disturbance to be expected as it is not induced by man. From a longer-term point of view, change in climate, whether wetter or drier, would have a profound impact upon plant species composition and primary productivity.

**Acknowledgment**

The authors wish to thank Virginia A. Uresk for helpful suggestions and technical advice during this study.

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## Association News

Plans for the spring meeting of the Association are going forward with increased speed. All indications are that president Ken Holmes and his many able helpers at Oregon College of Education are putting the finishing touches on a fine meeting.

There will be separate sessions in Botany, Chemistry-Physics, Geology-Geography, Science Education, Forestry, Zoology, Social Science, and Soil and Water. And don't forget the featured symposium on "Coastline Environment of the Pacific Northwest."

If you haven't sent your dues in, please do so soon.

Please encourage your colleagues and graduate students to attend the meeting.

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# Fourth Supplement to the Flora of Mount Shasta

**Abstract**

A list of 188 species of plants found on Mount Shasta, Siskiyou Co., California, is presented. Of these, 76 species are additions to previous published lists including the Flora and three supplements, four entries note taxonomic problem areas and species carrying the Shasta name but not occurring on the mountain, and 108 entries represent nomenclatorial changes for species entries on earlier lists.

During the summer of 1936 I started collecting vascular plants on Mount Shasta, Siskiyou Co., California. At first I was interested in gaining a knowledge of the plants which grew on that mountain, but later became interested in obtaining as large a representation of species as possible. During the production of the resulting lists, a "Flora of Mount Shasta" (Cooke, 1940), represented in the following list by the symbol (F), and its supplements (Cooke, 1941, 1949, 1963), represented by the symbols (1), (2), and (3), a lack of conformity with the standard reference literature developed. In addition, since the publication of the third supplement (Cooke, 1963), a number of species never before reported for the Mount Shasta area have been reported. These include several ephemeral adventive plants introduced to the area of the mountain by a series of events described by Frenkel (1967, 1974), some of which are noted for the concerned species listed below. Dr. Frenkel's voucher numbers are listed for each of his records. Most of these were deposited in the Herbarium of the California Academy of Sciences, San Francisco. Dr. McClintock and her assistant kindly checked the folders and noted in a preliminary survey those which had been mounted. These voucher numbers are in italics. Some voucher numbers are also in the Herbarium, Oregon State University, Corvallis. Cooke's collections are represented in herbaria with which persons making identifications are associated, including the University of California, Berkeley, and the New York Botanical Garden. Other herbaria with incomplete sets of Cooke specimens include those of Oregon State University, Washington State University, and the University of Cincinnati.

The arrangement in the following list is that used in the "Flora of Mount Shasta" (Cooke, 1940). For species listed for the mountain in the previously published papers cited, distributional data are not repeated although for several species they are amplified. However, nomenclature preferred in recent monographs, or in "A California Flora" (Munz and Keck, 1959), and its Supplement (Munz, 1968) are given. For species new to the list of plants appearing on the mountain, distributional data are given.

## Distributional Additions to the Flora of Mount Shasta

*Pinus jeffreyi* X *coulteri*—one of two types of hybrid pines planted in 1935-1939 in the chaparral fields on the southwest side of the mountain.

*Pinus radiate* -X *attenuata*—the second type of hybrid planted in the chaparral clearings on the southwest base of the mountain in 1935-1939.

*Sequoiadendron giganteum* (Lindl.) Buchh. A number of trees were planted near the Everitt

Memorial Highway terminating rows of planted pines. Growth is poor to luxuriant depending on individual sites which were chosen apparently for reasons unrelated to the needs of the trees.

*Agropyron cristatum* (L.) Gaertn. Collected by R. E. Frenkel (984, 985) in a small clearing near Everitt Point.

*Agropyron dasystachyum* (Hook.) Vasey. Collected by R. E. Frenkel (986) in a small clearing near Everitt Point.

*Agropyron elongatum* (Host.) Beauv. Collected by R. E. Frenkel (980, 987) in a small clearing near Everitt Point.

*Agropyron repens* (L.) Beauv. Collected by R. E. Frenkel (998) in a small clearing near Everitt Point.

*Agropyron trichophorum* (Link) Richt. Collected by R. E. Frenkel in a small clearing near Everitt Point.

*Agrostis tenuis* Sibth. Collected by W. B. & V. G. Cooke 34335, 12 July 1963, along the Everitt Memorial Highway at about 5,000 ft.

*Bromus laevipes* Shear. Collected by R. E. Frenkel (1009) at 5,355 ft along the Everitt Memorial Highway.

*Bromus orcuttianus* Vasey. Collected by R. E. Frenkel (227, 228, *229*) at E. and W., at 5,070 ft, Everitt Memorial Highway.

*Bromus pumpellianus* Scribn.? var. *tweedyi* Scribn. Collected by R. E. Frenkel (991) in a small clearing near Everitt Point.

*Bromus diandrus* Roth. Collected by R. E. Frenkel (236, *240*) west side of Everitt Memorial Highway at 4,235 ft.

*Bromus tectorum* L. var. *glabratus* Spencer. Collected by R. E. Frenkel (*231*) at 4,000 ft on the east and west side of the Everitt Memorial Highway.

*Cynodon dactylon* (L.) Pers. Reported by R. E. Frenkel from the Everitt Memorial Highway below 4,300 ft; and from a small clearing near Everitt Point (R. E. Frenkel 995, 996, 997).

*Dactylis glomerata* L. Collected by R. E. Frenkel (992) in a small clearing near Everitt Point.

*Eragrostis pilosa* (L.) Beauv. Collected by R. E. Frenkel (230, *882, 883,* 991) on the Everitt Memorial Highway at 4,000 ft on the west side of the road.

*Festuca ovina* var. *duriuscula* (L.) Koch. Collected by R. E. Frenkel (990) in a small clearing near Everitt Point.

*Holcus lanatus* L. Collected by V. G. & W. B. Cooke, 34340, 12 July 1963, Everitt Memorial Highway at about 5,000 ft. Identified by J. T. Howell.

*Hordeum jubatum* L. Collected by W. B. & V. G. Cooke, 17 July 1966, at Widow Springs, 5,000 ft.

*Lolium perenne* L. Collected by R. E. Frenkel (981, 993) in a small clearing near Everitt Point.

*Panicum capillare* L. var. *occidentale* Rydb. Collected by R. E. Frenkel (682, *880,* 882), Everitt Memorial Highway, 4,000 ft, on the west side of the road.

*Secale cereale* L. Collected by R. E. Frenkel (*241,* 245) at 4,235 ft, along the Everitt Memorial Highway on the west side of the road; and (988) in a small clearing near Everitt Point in 1968.

*Triticum aestivum* L. Observed at Horse Camp, 7,896 ft, as seedlings coming up from horse feed brought up with saddle and work horses. Climatic conditions at this elevation preclude the possibility of blooming of these plants, let alone fruiting.

*Carex festivella* Mkze. Collected by J. Major (643, 644), 14 July 1961, along Mud Creek at 1,980 m (6,000 ft). Identified by J. T. Howell who noted that the material was young.

*Carex jepsonii* J. T. Howell. Collected by J. Major (645), 14 July 1961, in Mud Creek Canyon at 1,980 m. Identified by J. T. Howell.

*Scirpus americanus* Pers. Leafing out annually, but never blooming, this perennial was probably introduced with some grass seed sent by a well-meaning visitor from Kentucky in the late 1920s. Mack Olberman, the first custodian of the Shasta Alpine Lodge, broadcast the seed near the water-supply outlet at Horse Camp, 7,896 ft, and a few square feet of non-blooming turf is produced annually.

*Lilium kelleyanum* Lemmon. It is probable that a large percentage of the population of leopard lilies listed in earlier reports as *L. pardalinum* are really *L. kelleyanum*. Careful field and herbarium studies are required to settle this point.

*Habenaria elegans* (Lindl.) Boland. Collected by R. E. Frenkel (688) in a chaparral clearing south of the entrance to the MacBride Springs area, south of the Everitt Memorial Highway.

*Phoradendron flavescens* (Pursh) Nutt. var. *macrophyllum* Engelm. Common on *Quercus kelloggii* below 4,000 ft on the south side of Mount Shasta, reaching up to and slightly above 4,000 ft at several points especially along the road from McCloud to Mud Creek Dam. Several collections of lichens made on older branches of a large plant form the basis of this record.

*Asarum caudatum* Lindl. Collected on alluvial soil in mixed conifer woods, Howard, 4,000 ft, W. B. & V. G. Cooke 49263, 21 August 1974. Identified by L. Heckard on basis of leaf shape and indument.

*Eriogonum hirtiflorum* Gray. Found once along the old logging road above Bolam Station, at approximately 5,000 ft, 16 July 1966. Identified by J. T. Howell.

*Polygonum aviculare* L. Frenkel found this species scattered on graded shoulders of the Everitt Memorial Highway at 3,861, 4,000, 5,070, and 5,500 ft (215, *226, 246,* 247, 252, 897, *898*).

*Polygonum convolvulus* L. This species was found at 3,861 ft along the Everitt Memorial Highway by Frenkel (249, 682).

*Polygonum sperguliaeforme* Meisen., collected by W. B. & V. G. Cooke 45412, 30 June 1972, in chaparral along the Military Pass Road above the Andesite Crossing, 5,000 ft. Identified by L. Heckard.

*Chenopodium atrovirens* Rydb. Found at about 5,000 ft along the Andesite Road, 1 July 1968, W. B. & V. G. Cooke 39230. Identified by L. Constance

*Chenopodium incognitum* H. A. Wahl. Collected by Frenkel (876) at 4,000 ft along the Everitt Memorial Highway.

*Chenopodium pumile* R. Br. Collected by Frenkel (871, *884,* 885) at 4,000 ft along the Everitt Memorial Highway.

*Saponaria officinalis* L. Found in chaparral along Everitt Memorial Highway at about 4,500 ft. W. B. & V. G. Cooke 49245, 20 August 1974.

*Brassica nigra* (L.) Koch. Frenkel found one stand of a few plants of this species (676) along the Everitt Memorial Highway at 4,210 ft.

*Descurainia pinnata* (Walt.) Britt. ssp. *halictorum* (Ckll.) Detl. Obtained along the Everitt Memorial Highway at 3,861 ft (Frenkel, 230), and at MacBride Springs (Frenkel, 286). Material (978, 979), probably of the subspecies, was also obtained near Everitt Point in 1968.

*Lepidum virginicum* L. var. *pubescens* (Greene) C. L. Hitchc. Found by Frenkel (*690, 877*) at 4,900 ft scattered on the shoulder of the Everitt Memorial Highway; also by W. B. & V. G. Cooke, 49242, at about 4,500 ft, 20 August 1974, the latter identified by L. Heckard.

*Horkelia tridentata* Torr. Collected by R. E. Frenkel (686, 687) in the vicinity of Howard, established in fine silty soil adjacent to the road at 4,000 ft. Collected by W. B. & V. G. Cooke 45457, 6 July 1972, near the Mud Creek Dam road at about 4,000 ft. Identified by L. Heckard.

*Malus sylvestris* Mill. (*Pyrus malus* L.) Two trees have become established, one near the spring near MacBride Springs, the other in the chaparral some distance southwest of MacBride Springs. The latter was found by a bulldozer operator who was preparing chaparral areas for replanting with pines. He thought it sufficiently novel that he let it stand and called the attention of his supervisor to it. Both trees bloom, and in some years both produce fruit of very low quality. The trees were probably between 15 and 25 years old when first noted and apparently started after the discarding of apple cores at the camp ground, or from moving traffic on the highway. W. B. & V. G. Cooke 35166, 11 July 1965. The tree at MacBride Springs was first noted 4 August 1967.

*Prunus persica* Batsch. One tree has become established along the Everitt Memorial Highway at about 4,500 ft. This area is open, dry, chaparral, to all appearances. Apparently the tree started from a seed which was discarded from a passing vehicle. The tree is apparently more than 15 years old and has never borne mature fruit to my knowledge. W. B. & V. G. Cooke 39264, 4 July 1968.

*Lotus nevadensis* Green. Collected by R. E. Frenkel (*285, 878*) along the Everitt Memorial Highway at 3,861 and 4,900 ft. This prostrate perennial becomes established on graded roadsides.

*Lotus purshianus* (Benth). Clem. & Clem. var. *glaber* (Nutt.) Munz. Noted by Frenkel at 4,000 ft along the Everitt Memorial Highway with *Erodium cicutarium* and *Panicum capillare.*

*Medicago lupulina* L. Collected by R. E. Frenkel (*680,* 701), along the Everitt Memorial Highway at 4,000 ft.

*Medicago sativa* L. Collected by R. E. Frenkel (976) near Everitt Point in 1968.

*Melilotus officinalis* (L.) Lam. Collected by R. E. Frenkel (*235*) at 4,235 ft along the Everitt Memorial Highway.

*Vicia villosa* Roth. Collected by R. E. Frenkel (*251, 681*) on the west side of the Everitt Memorial Highway at 4,000 ft.

*Acer negundo* L. ssp. *californicum* (Torr. & Gray) Wesmael. Collected by W. B. & V. G. Cooke in 1968. One plant has become established in a drainage area near the Everitt Memorial Highway at about 4,250 ft. This area is in a successfully established pine plantation and there may be an underground flow or seepage of water in the area. The tree appeared to be at least five years old in 1965, and in 1974 was still showing good growth.

*Oenothera deltoides* Torr. & Frem. subsp. *piperi* (Munz) Klein. Several plants occurred at a turnout on the south side of U.S. Highway 97 one mile east of Siskiyou Co. Route A-12, at about 4,060 ft, W. B. & V. G. Cooke 42692, 22 July 1970. Identified by Peter Raven.

*Oenothera hookeri* Torr. & Gray subsp. *angustifolia* (Gates) Munz. Collected by R. E. Frenkel at 4,000 ft and 4,235 ft, along the Everitt Memorial Highway.

*Linanthus ciliatus* (Benth.) Greene. Collected by W. B. & V. G. Cooke 35179, at about 5,000 ft along the Bolam Road above the railroad crossing at Bolam Station, 12 July 1965. Identified by R. Bacigalupi.

*Eriodictyon californicum* (Hook. & Arn.) Torr. Collected by W. B. & V. G. Cooke 42698, at about 3,500 ft, 7 miles northwest of Weed along U.S. Highway 97, northwest base of Mount Shasta, 22 July 1970.

*Phacelia cookei* Constance & Heckard. Collected by W. B. & V. G. Cooke at about 4,370 ft along the Andesite Road, Mt. Shasta, 22 July 1970. W. B. & V. G. Cooke 45419 was collected 30 June 1972 in and along this road up to 5,000 ft.

*Cryptantha ambigua* (Gray) Greene. Collected by W. B. & V. G. Cooke, 35169, along U.S. Highway 97 at the Whitney Creek turnout, and 35176 along the Bolam Road, Mt. Shasta, 12 July 1965. Identified by R. Bacigalupi.

*Cryptantha intermedia* (Gray) Greene. Collected by W. B. & V. G. Cooke 45410, 30 June 1972, along the Military Pass Road above Andesite Crossing in brush. Identified by L. Heckard.

*Collinsia torreyi* Gray var. *latifolia* Newsome. Collected by W. B. & V. G. Cooke, 45456, in moist area along road to Mud Creek Dam, south side of Mount Shasta, at about 3,750 ft, 6 July 1972. Identified by L. Heckard.

*Mimulus nanus* Hook. & Arn. Collected by W. B. & V. G. Cooke, 34263, and 34272, about 5,000 ft along the Bolam Road, 10 July 1963; and 37213 at about 4,500 ft along the Hotlum Road, 16 July 1966. These collections were identified by R. Bacigalupi. W. B. & V. G. Cooke 45418, collected 30 June 1972, along the Military Pass Road above the Andesite Crossing at about 5,000 ft, was assigned to var. *nanus* by L. Heckard.

*Plantago major* L. Collected by Frenkel (673) at 4,200 ft along the Everitt Memorial Highway on the east side of the shoulder.

*Heterocodon rariflorum* Nutt. Collected by W. B. & V. G. Cooke 49262, 21 August 1974, at Howard, 4,000 ft. On wet gravel bar in small stream draining City of Mount Shasta water supply spring. Identified by L. Heckard.

*Aster ledophyllus* (Gray) Gray. Collected by R. E. Frenkel (276) at 4,235 ft along the Everitt Memorial Highway on both east and west sides of the right-of-way.

*Balsamorrhiza deltoidea* Nutt. In open spaces between chaparral shrubs south of a turnout approximately one mile west of the Bolam Road about 3,600 ft, Mt. Shasta. W. B. & V. G. Cooke 42693, 22 July 1970.

*Centaurea virgata* Lam. var. *squarrosa* (Willd.) Beiss. Collected by R. E. Frenkel (684, *685, 875*) at 4,900 ft along the Everitt Memorial Highway. Forming a well-established stand at a pull-off on the south side of the road.

*Chaenactis douglasii* (Hook.) Hook. & Arn. Collected by W. B. & V. G. Cooke 34265, 35177, and 35192, at between 5,000 and 6,000 ft along the road above Bolam Station on dry, open, sandy slopes. The earlier collection was identified by A. Cronquist, the later by R. Bacigalupi. W. B. & V. G. Cooke 45408, 5,000 ft, 30 June 1972, was found in chaparral along the Military Pass Road above Andesite Crossing. Identified by L. Heckard.

*Cirsium pastoris* J. T. Howell. Collected by W. B. & V. G. Cooke 35167, 12 July 1965, and also on 16 July 1966, on the south side of U.S. Highway 97 at a turnout above Whitney Creek at about 4,000 ft. Collected by R. Frenkel (994) at 4,243 ft, east of Everitt Memorial Highway on section 33/4 road.

*Conyza canadensis* (L.) Cronq. var. *glabrata* (Gray) Cronq. Collected by W. B. & V. G. Cooke 34326, 12 July 1963, along the Everitt Memorial Highway at about 4,000 ft.

*Eriophyllum lanatum* (Pursh) Forbes var. *grandiflorum* (Gray) Jepson. Collected by W. B. & V. G. Cooke 34219, 9 July 1963, on a dry sandy bank of Cascade Gulch near MacBride Springs, 5,000 ft, Mt. Shasta. Identified by A. Cronquist.

*Grindelia camporum* Greene. Collected by R. E. Frenkel (868, *869*) along the Everitt Memorial Highway at 5,400 ft, west; one or two individuals had become established in roadside rubble.

*Helianthus annuus* L. Seedlings were noted by W. B. & V. G. Cooke in a highway service equipment turnout along U.S. Highway 97 at the Andesite Road junction in the summer of 1970. While the area appears to be dry, there was no sign of wilting in these seedlings, which were probably two weeks old. The seeds could have been dropped from vehicles transporting live fowl apparently to market.

*Helianthus annuus* subsp. *lenticularis* (Dougl.) Ckll. Found in chaparral along the Everitt Memorial Highway at about 4,300 ft. W. B. & V. G. Cooke 49243, 20 August 1974. Identified by L. Heckard.

*Lactuca scariola* L. var. *integrata* Gren. & Godr. Collected by R. E. Frenkel (*872*) at 5,300 ft along the Everitt Memorial Highway. Frenkel noted that while the species was included in (F), this woody variety was not differentiated.

*Machaeranthera shastensis* var. *glossophylla* (Piper) Cronq. & Keck. Collected by W. B. & V. G. Cooke 35191, 12 July 1965, at about 5,000 ft, on the Bolam Road. Reported from the same area in May-June, 1966, by R. Bacigalupi, who also identified this collection.

*Sonchus asper* L. Collected by R. E. Frenkel (673, *674, 675*) from 4,200 ft east, on the Everitt Memorial Highway.

*Tetradymia canescens* DC. Collected by W. B. & V. G. Cooke 38668, 7 August 1967, in chaparral on the south side of U.S. Highway 97 near the Whitney Creek turnout. Identified by A. Cronquist.

### Corrections, Comments, Eliminations

*Panicum* X *shastense* Scribn. & Merr. ex Spellenberg. The type and only location in which this hybrid between *P. scribnerianum* and *P. pacificum* is known is the Castle Crags, Shasta Co., Calif. (Spellenberg, 1970). It is thus not considered part of the Flora of Mount Shasta.

*Lilium washingtonianum* Kell var. *minus* Purdy. It is possible that the Shasta Lily, found throughout the chaparral at the base of Mount Shasta, should be assigned to this variety. The problem of whether a separate variety should be maintained for this population needs elucidation through critical study of a series of collections from various areas in which the species occurs. At present, cultivated white "Easter" lilies include genetic materials from white lilies from a number of geographic areas including, it has been said, progeny from Mount Shasta. It may be noted that it was once feared that the Mount Shasta population would be eliminated by bulb hunters who removed wagon loads of bulbs making it necessary to protect the population legally through

enactment of one of the earlier wild-flower protection laws. Massive disturbance of the chaparral areas where pine plantations were established in the 1960s has demonstrated the resistance of this species to such disturbance. Large numbers of plants appear annually in the windrows of shrubs and top soil moved to simplify planting of the pine seedlings. It should be noted that the protection laws are reported to be still in force.

*Plantago shastensis* Greene. Listed as *P. eriopoda* Torr. by Munz. Since this species was reported from the Shasta Valley, and was named apparently for the Valley rather than for the Mountain, it is not considered part of the Flora of Mount Shasta.

*Collinsia parviflora* Dougl. ex Lindl. In addition to the colony reported in (F) from the Wagon Camp Road above Bear Springs, specimens were collected along an old wagon road above Hotlum Station which was used by the Forest Service. The collection at the University of California, Berkeley, which was originally reported as *Gilia leptalea,* is correctly identified as *C. parviflora* by L. Heckard.

### Nomenclatorial Changes

Following monographic studies and floristic revisions, the names of certain taxa reported in the Flora and its supplements have been changed. While source materials for these changes are available to many students of the California flora, they are not available to others. Pending a complete revision of the Flora of Mount Shasta, these changes are presented herewith.

*Athyrium alpestre* (Heppe) Rylands var. *americanum* Butters, listed in (F) as *A. americanum* (Butters) Maxon.

*Pinus contorta* Dougl. var. *murrayana* Grev. & Balf. in A. Murr., listed in (F) as *P. contorta* var. *murrayana* Engelm., and in (2) as *P. contorta* var. *latifolia* Engelm.

*Pinus jeffreyi* Grev. & Balf. in A. Murr., listed in (F) as *P. ponderosa* var. *jeffreyi* Vasey.

*Pseudotsuga menziesii* (Mirb.) Franco. listed in (F) as *P. taxifolia* (Lamb.) Britt.

*Juniperus occidentalis* Hook. var. *occidentalis,* listed in (1) as *J. californica* Carr. var. *utahensis* Engelm.

*Juniperus communis* L. var. *saxatilis* Pall., listed in (F) as *J. communis* var. *montana* Ait.

*Calocedrus decurrens* (Torr.) Floria, listed in (F) as *Libocedrus decurrens* Torr.

*Agrostis variabilis* Rydb., listed in (F) as *A. rossae* Vasey.

*Poa suksdorfii* (Beal) Vasey ex Piper, includes material listed in (F) as *P. pringlei* Scribn.

*Carex scopulorum* Holm var. *bracteosa* (Bailey) J. F. Hermann, listed in (F) as *C. gymnoclada* Holm.

*Eleocharis palustris* (L.) R. & B., listed in (F) as *E. macrostachys* Britt.

*Luzula comosa* E. Mey., listed in (F) as *L. multiflora* (Ehrh.) Lejeune.

*Brodiaea lutea* (Lindl.) Mart. var. *analina* (Greene) Munz, listed in (2) as *Tritelia ixioides* (Ait. f.) Greene var. *analina* (Greene) Hoover.

*Calochortus tolmiei* H. & A., listed in (F) as *C. caeruleus* (Kell.) Wats. var. *maweanus* Jepson.

*Sisyrinchium greenei* Bickn., includes material listed in (F) as *S. bellum* Wats.

*Eburophyton austinae* (Gray) Heller, listed in (F) as *Cephalanthera austinae* (Gray) Heller.

*Goodyera oblongifolia* Raf., listed in (1) as *G. decipiens* (Hook.) Hubbard.

*Habenaria dilatata* (Pursh) Hook. var. *leucostachys* (Lindl.) Ames., listed in (F) as *H. leucostachys* (Lindl.) Wats.

*Alnus sinuata* (Regel) Rydb., listed in (F) as *A. viridis* DC. var. *sinuata* Regel.

*Chrysolepsis sempervirens* (Kell.) Hjelmquist, listed in (F) as *Castanopsis sempervirens* Dudley, and probably including material listed as *C. chrysophylla* A. DC.

*Phoradendron juniperinum* Engelm. var. *libocedri* Engelm. in Wats., listed in (F) as *Phoradendron libocedri* (Engelm.) Howell.

*Eriogonum marifolium* Torr. & Gray. This species now includes as a synonym *E. cupulatum* Stokes, a greenish flowered form which occurs near Wagon Camp.

*Eriogonum nudum* Dougl. ex Benth., listed in (F) as *E. latifolium* Smith in Rees subsp. *nudum* (Dougl.) Stokes.

*Eriogonum vimineum* Dougl. ex Benth. *ss. lat.,* listed in (F) as *E. baileyi* Wats.

*Polygonum newberryi* Small, listed in (F) as *P. davisiae* Brewer ex Gray as a result of an erroneous identification on my part.

*Rumex acetosella* L. Along Everitt Memorial Highway at about 4,500 ft in the chaparral, W. B. & V. G. Cooke 49244, 20 August 1974. Identified by L. Heckard.

*Rumex angiocarpus* Murbeck, listed in (F) as *R. acetosella* L. Correction based on a herbarium correction.

*Chenopodium berlanderi* Moq. var. *zscheckii* (Murr.) Murr., listed in (F) as *C. album* L. Quite common on graded road shoulders at 5,000 ft along the Everitt Memorial Highway at about ¼ mile uphill from MacBride Springs (Frenkel, 870).

*Salsola pestifer* A. Nels., listed in (2) as *S. kali* var. *tenuifolia* G. F. Mey.

*Sagina saginoides* (L.) Karst. var. *hesperica* Fern., listed in (F) as *S. linnaei* Presl.

*Stellaria calycantha* (Ledeb.) Bong. subsp. *interior* Hult., listed in (F) as *S. borealis* Bigl.

*Actaea rubra* Willd. subsp. *arguta* (Nutt.) Hult., listed in (F) as *A. spicata* L. var. *arguta* Torr.

*Delphinium nuttallianum* Pritz. ex Walp, listed in (F) as *D. pauciflorum* Nutt.

*Arabis rectissima* Greene. Frenkel voucher numbers 670, 671 and 672 were collected along

the Everitt Memorial Highway between 4,800 and 5,000 ft, near MacBride Springs, especially on the southwest side of the road. These specimens were found growing with *A. holboellii* var. *retrofracta.* A specimen in the Jepson Herbarium (Jepson 59c) was collected on Black Butte.

*Camelina microcarpa* Andrs., listed in (F) as *C. sativa* (L.) Crantz. Frenkel (*259*) collected this specimen at 4,235 ft. He noted that in 1963 and 1964 only a few plants were seen. In 1968 he collected this species (*982, 983*) in a small clearing below the old toboggan shed near Everitt Point, site of the multiple use demonstration area.

*Erysimum perenne* (Wats. ex Cov.) Abrams. This species includes *E. asperum* (Nutt.) DC. It was listed in (F) as *E. asperum* var. *perenne* S. Wats. in Cov.; it has been determined by several cooperators as *E. capitatum* (Dougl.) Greene; and specimens at the Herbarium, University of California, Berkeley, were noted by Rossbach as *E. capitatum* var. *perenne* (S. Wats.) G. B. Rossbach.

*Lepidium campestre* (L.) R. Br. Found by Frenkel (977) near Everitt Point in 1968.

*Streptanthus tortuosus* Kell. var. *orbiculatus* (Greene) Hall, listed in (F) as *S. orbiculatus* Greene.

*Amelanchier pallida* Greene, listed in (F) as *A. alnifolia* Nutt.

*Fragaria platyetala* Rydb., listed in (F) as *F. virginica* Duch. var. *platypetala* Hall.

*Holodiscus microphyllus* Rydb. var. *glabrescens* (Greene) Lay., listed in (F) as *H. discolor* (Pursh) Maxim var. *glabrescens* Heller.

*Horkelia densiflora* (Greene) Rydb., listed in (3) as a synonym, *H. pulchra* Rydb., reportedly collected on Mount Shasta.

*Sibbaldia procumbens* L., listed in (F) as *Potentilla sibbaldii* Hal. f.

*Astragalus curvicarpus* (Heller) Macbr., listed in (1) as *A. whitedii* Piper

*Lotus oblongifolius* (Benth.) Greene var. *nevadensis* (Gray) Munz, listed in (F) as *L. oblongifolius* var. *torreyi* (Gray) Ottley.

*Lotus purshianus* (Benth.) Clem. & Clem. var. *purshianus,* listed in (F) as *L. americanus* (Nutt.) Bisch. var. *minutiflorus* Ottley.

*Lupinus arbustus* Dougl. in Lindl. subsp. *silvicola* (Heller) D. Dunn., listed in (1) as *L. laxiflorus* Dougl. and *L. laxiflorus* var. *silvicola* (Heller) C. P. Smith.

*Lupinus confertus* Kell., listed in (3) as *L. lepideus* Dougl. var. *torreyi.*

*Lupinus latifolius* J. G. Agardh var. *viridifolius* (Heller) C. P. Smith, listed in (3) as *L. rivularis* Dougl. var. *viridifolius* Jepson.

*Lupinus ornatus* var. *obtusilobus* (Heller) C. P. Smith, listed in (3) as *L. obtusilobus* Heller.

*Lupinus polyphyllus* Lindl. subsp. *superba* (Heller) Munz, listed in (F) as *L. superbus* Heller var. *elongatus* C. P. Smith.

*Lupinus sellulus* Kell. subsp. *ursinus* (Eastw.) Munz, listed in (1) as *L. laxiflorus* Dougl.

*Trifolium longipes* Nutt. subsp. *hansenii* (Greene) Gillett, listed in (F) as *T. longipes* Nutt. For an analysis of the *T. longipes* complex see Gillett (1969).

*Trifolium wormskjoldii* Lehm., listed in (F) as *T. involucratum* Ort. var. *fimbriatum* McDerm.

*Linum perenne* L. subsp. *lewisii* (Pursh) Hult., listed in (F) as *L. lewisii* Pursh.

*Rhus trilobata* Nutt. ex Torr. & Gray var. *quinata* Jepson, listed in (1) as *R. trilobata* Nutt.

*Acer glabrum* Torr. var. *torreyi* (Greene) Smiley, listed in (F) as *A. glabrum* Torr.

*Malva neglecta* Wallr., listed in (F) as *M. rotundifolia* L.

*Circaea alpina* L. var. *pacifica* (Asch. & Moq.) Jones, listed in (F) as *C. pacifica* Asch. & Moq. Collected near the Mud Creek Dam Road along a spring creek at about 3,750 ft, 6 July 1972, by W. B. & V. G. Cooke 45455.

*Clarkia purpurea* (Curt.) Nels. & Macbr. subsp. *quadrivulnera* (Dougl.) Lewis & Lewis, listed in (F) as *Godetia quadrivulnera* (Dougl.) Stack. Also found in brush along the Military Pass Road above the Andesite Crossing at about 5,000 ft, 30 June 1972, by W. B. & V. G. Cooke 45411. Identified by L. Heckard.

*Epilobium anagallidifolium* Lam., listed in (F) as *E. alpinum* L.

*Epilobium exaltatum* E. Drew, listed in (F) as *E. glandulosum* var. *exaltatum* (Drew) Munz.

*Epilobium pringleanum* Hausskn., listed in (F) as *E. brevistylum* var. *subfalcatum* (Trel.) Munz.

*Gayophytum diffusum* subsp. *parviflorum* Lewis & Szwykowski, includes material listed in (1) as *G. lasiospermum* Greene, and in (1) as *G. nuttallii* Torr. & Gray.

*Gayophytum heterozygum* Lewis & Szwykowski. Probably the commonest collected species in this genus; most of the earlier collections were reported as *G. ramosissimum* Torr. & Gray.

*Gayophytum racemosum* Torr. & Gray, listed in (F) as *G. helleri* var. *glabrum* Munz.

*Gayophytum ramosissimum* Torr. & Gray. According to the revision of *Gayophytum* (Lewis & Szwykowski, 1964), this species is rare in Siskiyou Co. On the basis of matching specimens at the University of California, Berkeley, R. Bacigalupi decided that the specimen from W. B. & V. G. Cooke 37219, 16 July 1966, from 5,000 ft along a road above Bolam Station, compared favorably with material identified by Lewis & Szkykowski from east of Meyten in the Shasta Valley, Siskiyou Co., Calif.

*Perideridia parishii* (Coult. & Rose) Nels. & Macbr. subsp. *latifolia* (A. Gray) Chuang & Constance, listed in (F) as *Carum gairdneri* Gray.

*Pteryxia terebinthinus* (Hook.) C. & R. var. *californica* (C. & R.) Mathias, listed in (F) as *Cymopterus terebinthinus* (Hook.) T. & G.

*Sanicula graveolens* Poepp. ex DC., listed in (2) as *S. nevadensis* Wats.

*Kalmia polifolia* Wang. var. *microphylla* (Hook.) Rehl., listed in (F) as *K. polifolia* Wang.

*Chimaphila umbellata* Barton var. *occidentalis* (Rydb.) Blake, listed in (F) as *C. umbellata* Nutt.

*Vaccinium nivicitum* Camp, listed in (F) as *V. caespitosum* Michx.

*Pyrola picta* var. *picta* forma *aphylla* (Sm.) Camp, listed in (F) as *P. aphylla* Sm.

*Pyrola picta* subsp. *integra* (Gray) Piper, listed in (F) as *P. dentata* var. *integra* Gray.

*Pyrola secunda* L., listed in (2) as *Ramischia secunda* (L.) Gaertn.

*Trientalis latifolia* Hook., listed in (F) as *T. europaea* L. var. *latifolia* Torr.

*Frasera albicaulis* (Griseb.) Kuntze, listed in (1) as *Swertia albicaulis* Dougl., and in (3) as *S. shastensis* St. John.

*Apocynum pumilum* (Gray) Greene, listed in (F) as *A. androsaemifolium* L. var. *pumilum* Gray.

*Ipomopsis aggregata* (Pursh) V. Grant, listed in (F) as *Gilia aggregata* (Pursh) Spreng., and including material cited in (2) as *G. aggregata* ssp. *formosissima* (Greene) Wherry, and in (2) as *G. texana* (Greene) Wood. & Standl.

*Microsteris gracilis* (Dougl. ex Hook.) Greene, listed in (F) as *Phlox gracilis* (Hook.) Greene.

*Phlox diffusa* Benth., includes *P. diffusa* subsp. *typica* Wherry, listed in (2), which includes *P. douglasii* Hook., listed in (F).

*Polemonium pulcherrimum* Hook., listed in (F) and (3) as *P. shastense* Eastwood.

*Phacelia hastata* Dougl. ex Lemmon, listed in (F) as *P. leucophylla* Torr. ex Frem.

*Phacelia hastata* Dougl. ex Lemmon X *heterophylla* Pursh. Based on a report in Heckard (1960).

*Phacelia heterophylla* Pursh, listed in (F) as *P. californica* Cham. var. *virgata* (Greene) Jepson (but see above entry).

*Mimulus breweri* (Greene) Cov., listed in (1) as *M. rubellus* var. *breweri* (Gray) Greene.

*Mimulus muschatus* Dougl. ex Lindl. var. *moniliformis* (Greene) Munz, listed in (F) as *M. muschatus* Dougl., and in (2) as *M. maniliformis* Greene.

*Pentstemon davidsonii* Greene, listed in (F) as *P. menziesii* Hook. var. *davidsonii* (Greene) Piper.

*Veronica alpina* L. var. *alterniflora* Fern., listed in (F) as *V. alpina* var. *cascadensis* Fern., and in (2) as *V. wormskjoldii.* var. *alterniflora* (Fern.) Pennell.

*Orobanche fasciculata* Nutt. subsp. *lutea* (Perry) Achey, listed in (1) as *O. fasciculata* Nutt. In recent correspondence, Heckard indicates that this subspecies is probably without taxonomic significance.

*Linnaea borealis* L. subsp. *longiflora* (Torr.) Hult., listed in (1) as *L. borealis* var. *americana* Rehder.

*Sambucus microbotrys* Rydb., listed in (F) as *S. racemosa* L.

*Agoseris aurantiaca* (Hook.) Greene, listed in (F) as *A. gracilens* (Gray) Ktze.

*Antennaria alpina* (L.) Gaertn. var. *media* (Greene) Jepson, listed in (2) as *A. media* Greene.

*Antennaria neglecta* Greene var. *howellii* (Greene) Cronq. Identified by a cooperator as *A. howellii* Greene.

*Aster occidentalis* (Nutt.) T. & G., listed in (F) but now includes *A. fremontii* (T. & G.) Gray also listed in (F).

*Chrysothamnus nauseosus* (Pall.) Britt. var. *albicaulis* (Nutt.) Hall & Clem., listed in (F) as *C. nauseosus* var. *occidentalis* (Greene) Hall.

*Cirsium vulgare* (Savi) Thomas, listed in (F) as *C. lanceolatum* (L.) Scop.

*Conyza canadensis* (L.) Cronq. var. *canadensis,* listed in (F) as *Erigeron canadensis* L. With the identification of the variety listed above occurring with adventives along the Everitt Memorial Highway, it is suggested that material collected in the chaparral at the base of the Sisson Southern Trail at about the location where horses were tethered for loading for the trip to Horse Camp represents the typical variety of the species.

*Erigeron inornatus* Gray var. *viscidulus* Gray, listed in (F) as *E. inornatus* Gray.

*Eriophyllum lanatum* (Pursh) Forbes var. *achillaeoides* (DC) Jepson. Collected by W. B. & V. G. Cooke 45420, 30 June 1972, at about 5,000 ft along the Military Pass Road above the Andesite Crossing.

*Gnaphalium microcephalum* Nutt. var. *thermale* (E. Nels.) Cronq., listed in (F) as *G. microcephalum* Nutt.

*Haplopappus bloomeri* Gray, listed in (F) (3) as *Chrysothamnus bloomeri* Gray var. *angustatus* Gray.

*Senecio canus* Hook., listed in (F) as *S. howellii* Greene and *S. oreopolis* Greene. While *S. cymbalariodes* Nutt. was used in (F) and (I) and by Munz, it is now considered part of this species. Also collected by W. B. & V. G. Cooke 45421 in chaparral along the Military Pass Road at about 5,000 ft, above Andesite Crossing, 30 June 1972. Identified by L. Heckard. Earlier records had been obtained at and above timberline.

*Solidago canadensis* L. subsp. *elongata* (Nutt.) Keck, listed in (F) as *S. elongatus* Nutt.

*Stephanomeria paniculata* Nutt., listed in (F) as *S. virgata* Benth.

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# Intraspecific Variation in Brodiaea douglasii Watson (Liliaceae)

**Abstract**

Intraspecific variation in certain morphological, cytological and phenological characteristics of *Brodiaea douglasii* (Liliaceae) was examined to ascertain its taxonomic significance. Analysis of variance showed that statistically significant differences exist between native populations with respect to the morphological characters used. Duncan's Multiple Range Test, however, indicated that in the species as a whole, the pattern is one of overlapping variation rather than one of groups of populations. At the 10 percent significance level, corm depth was the only character that separated the populations into two groups.

*B. douglasii* has a base number of $x = 8$ and plants with $2n = 16$, 24, 32, 40, 48 and 56 were found. Diploids and polyploids tend to be morphologically distinct, the polyploid plants being more robust. The polyploids also tend to flower later and to produce more vegetative offspring than do diploids. The two ploidy classes generally occupy different habitats. This ecological separation enhances the morphological differences between polyploids and diploids.

## Introduction

*Brodiaea douglasii* Watson is a spring flowering plant native to the sagebrush steppe and adjacent woodlands of the Pacific Northwest. Its range extends from southern British Columbia to southern Oregon from the eastern slopes of the Cascades to western Montana and Wyoming. Like other species of the genus, *B. douglasii* is a scapose, perennial herb. At maturity, each corm produces 2 leaves and a single flowering stalk which bears several blue flowers. Reproduction occurs through division of the corm, by production of numerous cormlets, and by seed. Seeds and immature corms produce just one leaf during the growing season.

The species belongs to the subgenus *Triteleia* (Doug. ex Lindl.) Munz of *Brodiaea* Smith sensu Hitchcock *et al.* (1969). The most recent monograph of this subgenus is that of Hoover (1941). He described *B. douglasii* as remarkably uniform apart from indications of hybridization with *B. howellii* Watson in the East. The study reported here was stimulated by an observation of the late Dr. Marion Ownbey (pers. comm.) that in Asotin County, Washington, there are very distinct forms of *B. douglasii.* Moreover, at some locations, these forms grow sympatrically with little or no evidence of hybridization between them.

None of the variation observed in Asotin County suggests introgression by another species. The only species with which hybridization might have occurred are *B. howellii* and *B. hyacinthina* (Lindl.) Baker. Intermediates between *B. howellii* and *B. douglasii* were observed by Hoover in Yakima County (1955), but it lies 150 mi to the west of Asotin County and is the eastern limit of the range of *B. howellii.* The range of *B. hyacinthina* includes southeastern Washington, but this species flowers six to eight weeks later than *B. douglasii.* Furthermore, on morphological grounds it is extremely unlikely that either *B. howellii* or *B. hyacinthina* is responsible for the variation in *B. douglasii* observed in southeastern Washington. Accordingly, this study of the variation in *B.*

*douglasii* was limited to populations of the species itself. It was undertaken to examine the nature and extent of the variation in and between populations of *B. douglasii* in order to determine whether recognition of subspecific taxa is merited. Various morphological, phenological, and cytological aspects of the species were examined.

### Methods and Materials

*Sampling.* In 1972, 1973, and 1974 I obtained population samples of *B. douglasii* from localities in Washington, Idaho, and Oregon (Figs. 1, 2). A sample consisted of up to 50 flowering shoots and corms. If two distinct forms were growing in the same location, each was treated as a separate population for sampling purposes. To lessen the probability of collecting several shoots from the same clone, only plants growing at least a meter apart were included in the sample. Notes were made of the associated vegetation and soil conditions at each site.

*Morphology.* Ten measurements were made on each of the shoots in the population samples: peduncle length, corm depth, leaf length, leaf width, number of flowers in the inflorescence, pedicel length, perianth length, hypanthium length, distance between the insertion of the upper and lower stamen filaments, and stipe length. The last six measurements were made on whichever flower in the inflorescence was considered to be closest to anthesis. The data were initially examined by analysis of variance, to determine whether the differences between the collection means were statistically significant. Duncan's New Multiple Range Test, modified to accommodate unequal sample

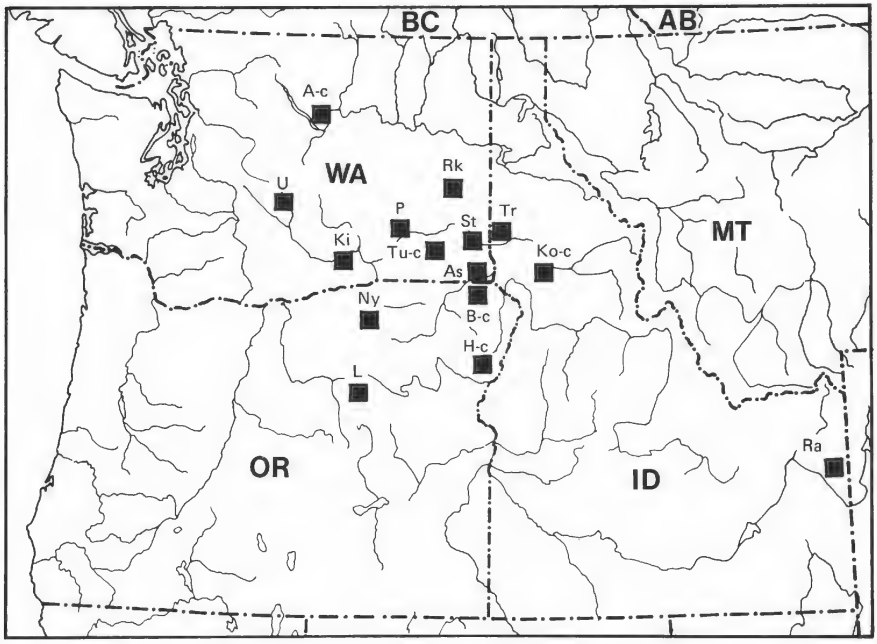


Figure 1. Location of sampled populations of *Brodiaea douglasii.* c, only corms collected; A, Alta Lake; As, several sites, see Figure 2; B, Buford Ridge; H, Halfway; Ki, Kiona; Ko, Kooskia; L, Long Creek; P, Palouse Falls; Ra, Rainy Pass; Rk, Rock Lake; St, Steptoe; Tr, Troy Road; Tu, Tucannon; U, Umtanum.

sizes (Steel and Torrie, 1960), was then applied to determine which collection means were significantly different.

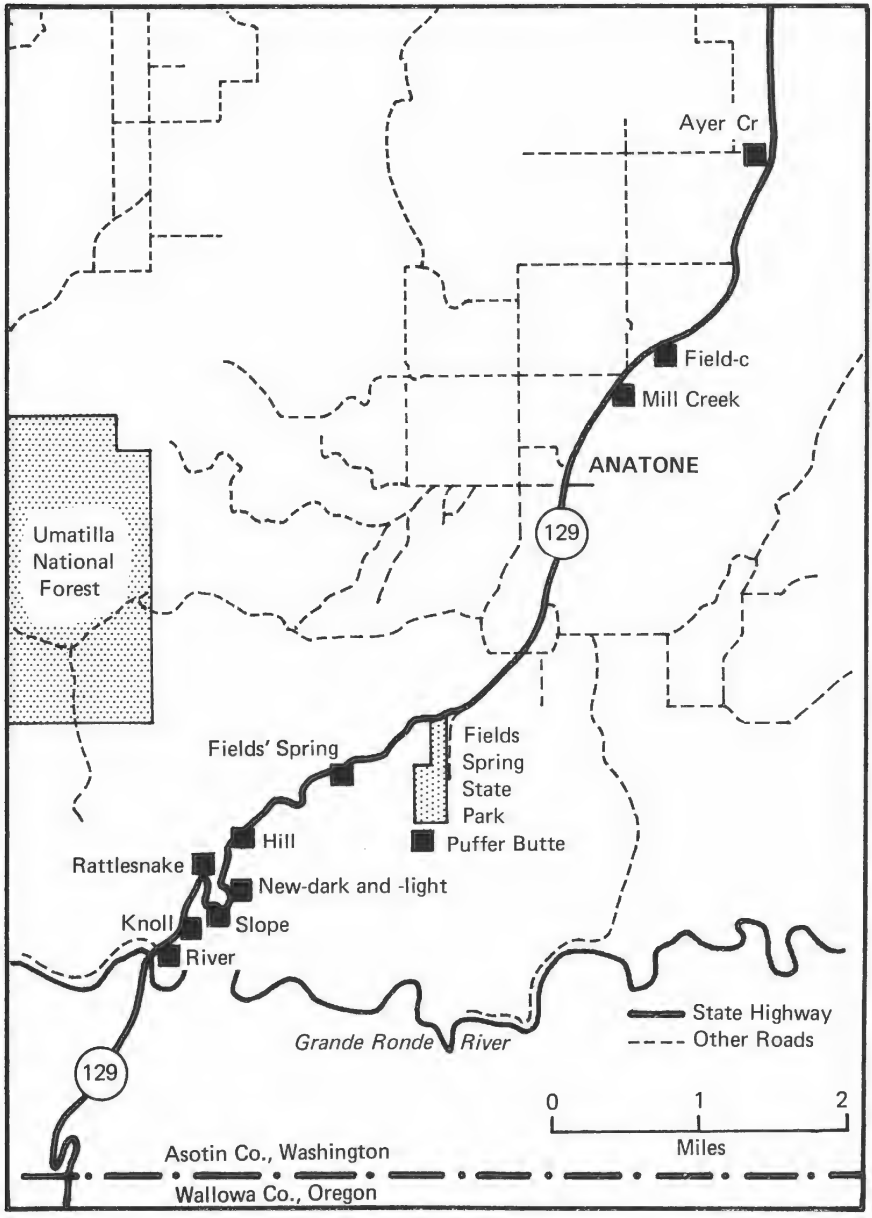


Figure 2. Location of sampled populations of *Brodiaea douglasii* in Asotin County, Washington. (c: only corms collected.)

*Cytology.* Both root tip and pollen mother cells were used in the cytological studies. Root tips were obtained from corms grown on the surface of damp sandy soil placed in a cool greenhouse. The tips were held in 0.1 percent colchicine for 4-6 hr prior to hydrolysis in 50 percent HCl for 7 min at room temperature. They were then rinsed, stained in acetocarmine, and squashed. Pollen mother cell preparations were made by squashing immature anthers in acetocarmine without prior fixation. All slides were made semi-permanent by ringing the coverslips with Massart's solution and allowing the slide to dry for 24 hr at room temperature. Differentiation of the chromosomes improved during this time so critical examinations were made after the slides had dried. Drawings were prepared with the aid of a camera lucida.

*Phenology.* Observations were made on the growth of *B. douglasii* at different stages of its life cycle and under various conditions. Corms planted in the experimental gardens at Pullman, Washington, primarily as a source of cytological material, were dug up after two years and the number reproducing vegetatively noted. Similar observations were made on corms grown in the greenhouse as a source of root tip material.

Seeds were germinated in the dark on damp filter paper. The seeds were kept at 4C and the number germinating each week was recorded.

In 1974, weekly observations were made of the leaf and peduncle growth of plants in four native populations of *B. douglasii* in Asotin County, Washington. The populations were chosen to include representatives of both forms of the species growing in the area. Records were maintained until flowering occurred. At that time, the proportion of flowering and non-flowering plants of *B. douglasii* in each location was recorded.

#### Results

The characteristics of the populations are summarized in Figure 3. The idiograms are stylistic representations of the flowers and shoots in each sample. Each dimension of the idiogram for a particular collection is proportional to the mean value of one of the measured characteristics in that sample. Which character each dimension represents can be determined by reference to the key figure. The characters are not all drawn to the same scale, but for a given character, the same scale is used in each idiogram. Thus, the idiograms can be used to make comparisons between populations. Moreover, leaf length is drawn to the same scale as peduncle length and perianth length to the same scale as the hypanthium. Flower number refers to the average number of flowers per inflorescence in a given sample.

As can be seen, certain characteristics tend to be associated. Plants with short, narrow leaves generally have fewer flowers, proportionately longer peduncles, and shallower corms than do plants with long, wide leaves. The populations do not, however, fall into distinct groups on the basis of these characteristics. There is some overlap between individuals of the various populations. Stipe length and filament insertion vary considerably between the populations but are not obviously associated with any of the other measured characters.

Some populations were sampled in both 1972 and 1973. In each instance, the plants in the 1973 collection had somewhat shorter leaves than those collected in 1972. This finding can be attributed to such factors as different weather conditions, sampling patterns, and possibly differences in the developmental stage of the population at the time of collection.

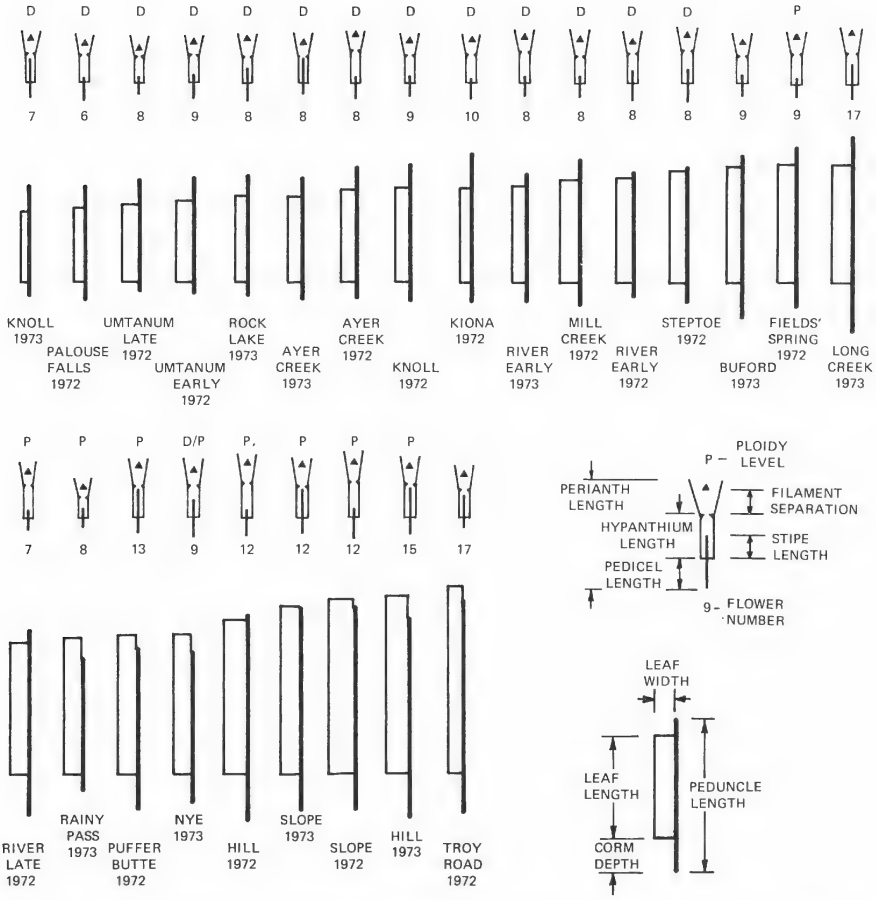


Figure 3. Idiographic representation of the characteristics of the sampled populations of *Brodiaea douglasii*. See text for further explanation.

The F ratios obtained from the analysis of variance indicated that, for each character, the differences in the collection means were significant at the 0.5 percent level of confidence. Analysis of variance is not, however, designed to reveal which means within a set are significantly different. Duncan's Multiple Range Test does do so. For each of the characters examined in this study, Duncan's Multiple Range Test identified some populations that were significantly different at the 5 percent level. No characteristic, however, divided the collections into sets such that all the collections in one set were significantly different from each of those in the other set. One characteristic, corm depth, did so at the 10 percent level (Fig. 4).

It became evident that much of the variation observed is associated with differences in ploidy level. Most populations of small plants are diploid whereas those of large plants are usually polyploid. The collection means were examined to determine whether, for any character, the means of all the diploid collections were consistently higher or

lower than those of the polyploid collections. It was so for corm depth and leaf length, both of which are greater in polyploid populations. Nevertheless, of the two sets into which the collections are separated by Duncan's Test on the basis of corm depth, one set contains only polyploid populations, but the other contains one polyploid population (Fields' Spring) in addition to all the diploid populations. Leaf length did not separate the collections into sets at the 10 percent significance level (Fig. 5).

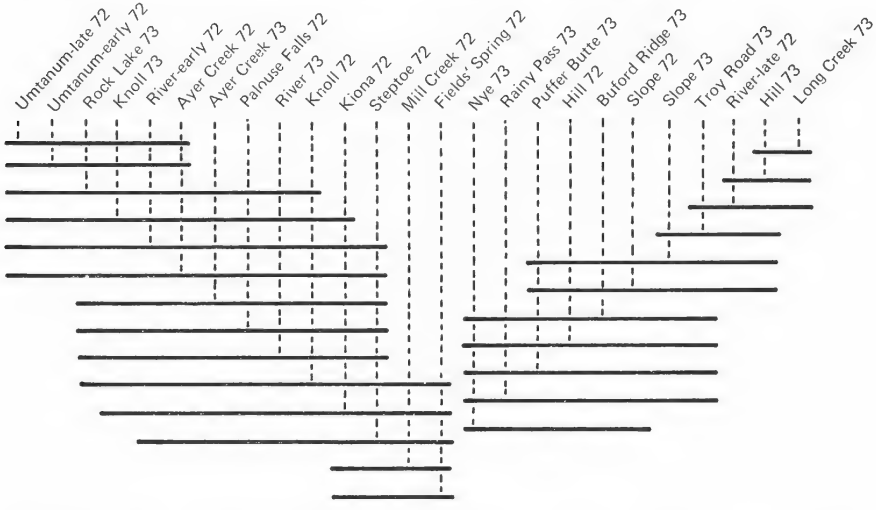


Figure 4. Results of Duncan's Multiple Range Test for corm depth. Collections not underscored by the same line had means that were significantly different at the 10 percent level.

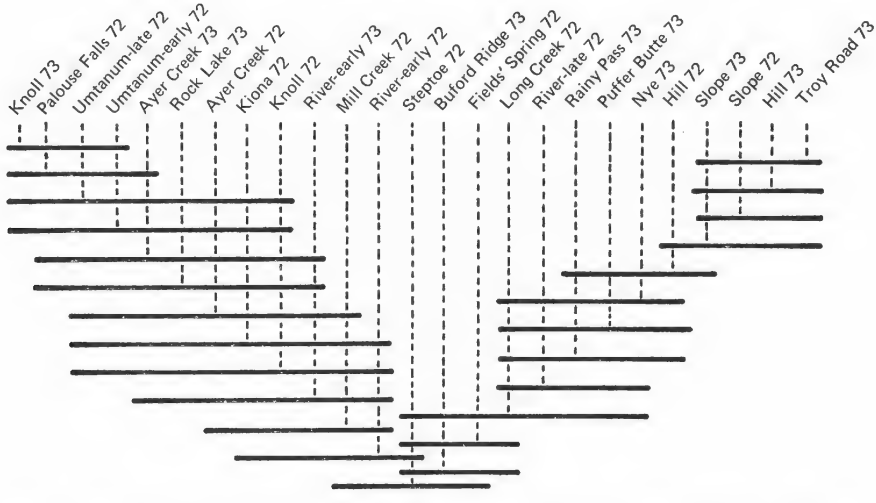


Figure 5. Results of Duncan's Multiple Range Test for leaf length. Collections not underscored by the same line had means that were significantly different at the 10 percent level.

*Cytology.* The base number in *B. douglasii* is x = 8. The species exists at the diploid, triploid, tetraploid, and hexaploid levels (Table 1). It is possible that other chromosome levels may be present in the species. The quality of the preparations obtained from several plants precluded the making of an accurate count although it was evident the plant was polyploid.

No consistent variation in karyomorphology was observed, nor was it possible to identify "marker" chromosomes that would serve to identify a particular genome. Representative sets of mitotic chromosomes are shown in Figures 6 to 8. The only previous count for the species is that of Burbanck (1941) who reported 2n = 32.

Meiosis was regular in all the diploid cells examined (Fig. 9), but several irregularities were observed in polyploid cells. Univalent and multivalent formations were fairly common, the latter involving as many as six chromosomes in some instances. The multivalents occasionally formed rings or chains at metaphase I (Fig. 10). Lagging was also a common occurrence in polyploid cells (Fig. 11).

*Phenology.* Plants grown in the experimental garden at Pullman, Washington, exhibited the same overall morphology as was observed in the field. This similarity was true both in 1973 and 1974, indicating the observed variation is indeed genetic and does not merely reflect the environmental influences on the quantity or quality of metabolites stored in the corms during the previous growing season.

Some of the corms failed to produce a flowering shoot until their second year in the garden, producing just one leaf in the intervening year. A pair of leaves is produced

TABLE 1. Chromosome counts for poulations of *Brodiaea douglasii.*

| Population | Source | |
|---|---|---|
| | Pollen mother cell | Root tip cells |
| Alta Lake | n=8 | 2n=16 |
| Ayer Creek | n=8 | 2n=16 |
| Knoll | n=8 | 2n=16 |
| Kooskia | n=8, ca 14 | |
| Mill Creek | n=8 | |
| New-dark | | 2n=16 |
| Nye | n=8, ca 16 | 2n=16, 32 |
| Palouse Falls | n=8 | 2n=16 |
| River-early | n=8 | 2n=16 |
| Rock Lake | n=8 | |
| Steptoe | n=8 | 2n=16 |
| Umtanum | | 2n=16 |
| Field | | 2n=32, ca 38 |
| Fields' Spring | n=ca 24 | 2n=ca 38, ca 48 |
| Halfway | n=16 | 2n=32 |
| Hill | n=16, 24 | 2n=48, 56 |
| Mill Creek South | | 2n=32 |
| Mill Road | | 2n=32 |
| Puffer Butte | | 2n=24, 32, 40, ca 45 |
| Rainy Pass | | 2n=32 |
| Rattlesnake | | 2n=ca 32 |
| River-late | | 2n=40 |
| Slope | n=16, 24 | 2n=48 |
| Tucannon | | 2n=32 |

Figures 6-11. Chromosomes of *Brodiaea douglasii*. 6. Mitotic metaphase, Kiona, $2n=16$. 7. Mitotic metaphase, Mill Creek, $2n=32$. 8. Mitotic metaphase, Puffer Butte, $2n=40$. 9. Meiotic metaphase, Knoll. 10. Meiotic metaphase, Fields' Spring. 11. Meiotic metaphase, Hill.

when a flowering shoot is developed. None of the immature cormlets transplanted to the garden developed a flowering shoot during the two years of the study.

Very few of the corms reproduced vegetatively in the garden. In 1974 corms from only six populations, five diploid and one polyploid, were found to be dividing. Moreover, the largest number of new corms formed by a single corm was three. By contrast, almost all the polyploid corms grown on sand in the greenhouse produced several cormlets, generally more than three and, in one instance, as many as 14. A few of the diploid corms in the greenhouse did divide, but as in the garden, they usually formed just two, occasionally three, slightly smaller corms. Contractile root formation in the greenhouse was also almost completely limited to polyploid corms and cormlets. Diploid corms rarely produced such roots even though growing under identical conditions.

Field observations concerning vegetative reproduction paralleled the situation in the greenhouse rather than that in the garden and was reflected in the ratio of flowering to non-flowering shoots present in native populations. In two polyploid populations for which counts were made, Slope and Hill, the ratios obtained were 18:51 and 9:107 respectively; for two diploid populations, River-early and Knoll, the corresponding figures were 27:10 and 36:8 respectively.

Both diploid and polyploid plants produce good seed. The seeds are slow to germinate under the conditions used. Only one seed germinated during the first 21 days and six did so between the 73rd and 88th days. Most took about 50 days. In the two diploid populations tested, Ayer Creek and Kiona, the germination rates were 97 percent and 95 percent respectively. Seeds from three polyploid populations tested, Puffer Butte, Troy Road, and Tucannon, gave germination figures of 94 percent, 82 percent, and 73 percent respectively. It should be noted that only plump, firm seeds were used; immature, empty, or rotten seeds were discarded. No counts were made of the number of "good" seeds produced per plant.

Successful sexual reproduction requires not only that the seeds produced germinate but also that the seedlings themselves develop into fruiting plants. This process, according to the garden observations, takes at least three years in *B. douglasii.* No attempt was made to grow seedlings to maturity in this study, nor was the possibility of apomictic seed production investigated. Consequently, it is not possible to state definitely whether reproduction by seed is successful.

Leaf growth was far more rapid in the Hill and Slope populations, which are polyploids, than in the Knoll and River-early populations which are both diploid (Fig. 12). The peduncle growth rate, however, is essentially the same in all four populations (Fig. 12), but the final height is greater in the polyploid populations. Furthermore, the peduncle of polyploid plants is not visible until the leaves are about 30 cm long whereas in diploid plants, it reaches ground level when the leaves are about 10-15 cm long.

#### Discussion

Morphological variation within *B. douglasii* is indeed very limited, consisting mainly of differences in the size and proportions of various plant organs. The plants at a particular site are usually very uniform not only with respect to their absolute dimensions but also in terms of their proportions. Although striking differences do exist between individual populations, the pattern within the species is of overlapping patterns of variation so that in the species as a whole the morphological variation forms a continuum.

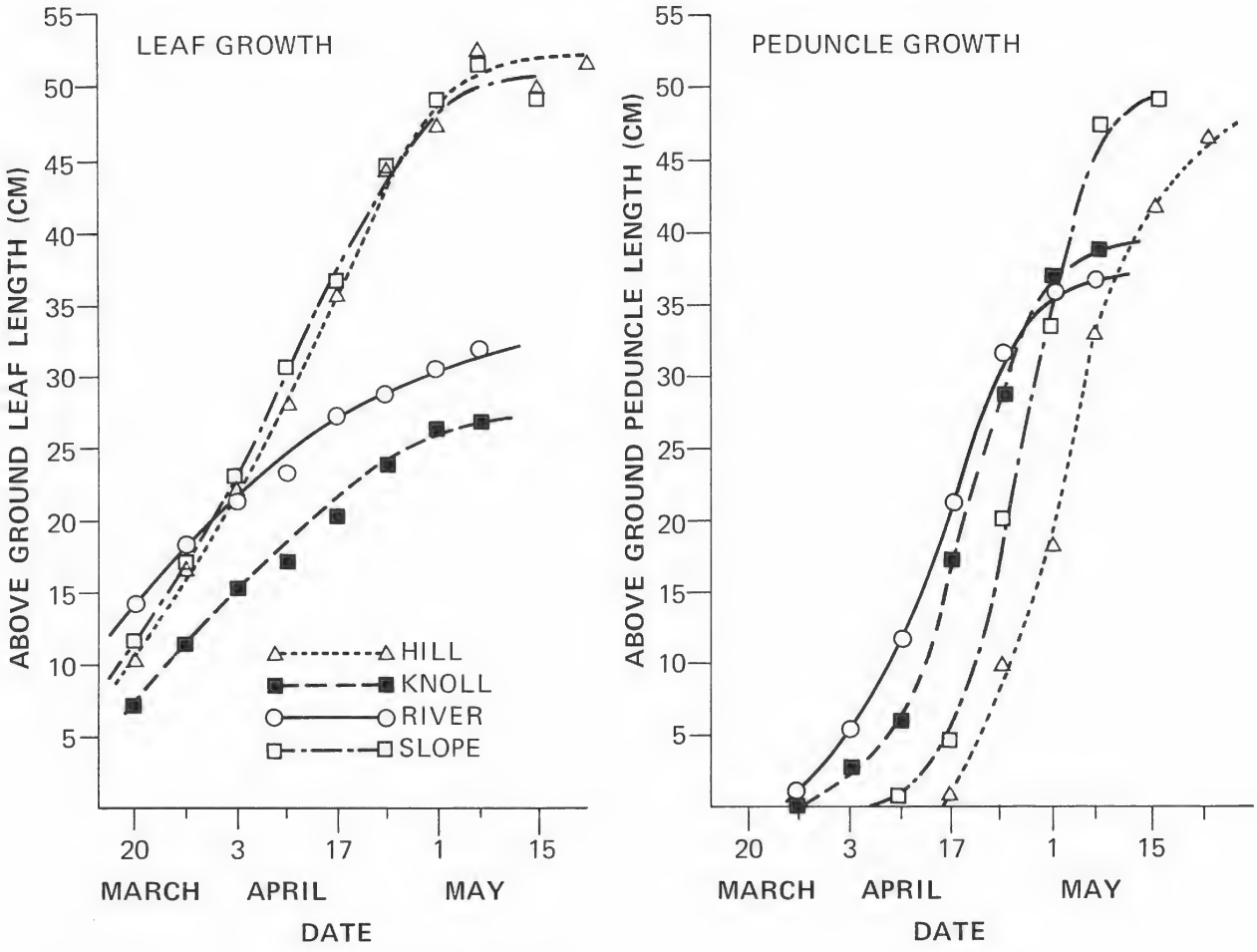


Figure 12. Leaf and peduncle growth in *Brodiaea douglasii*.

Initially the populations studied were designated "robust" or "small". These designations were based on overall size, the ratio of peduncle to leaf length, and the number and color of the flowers. During the course of the study additional characters were found to be associated with the two forms. "Robust" plants flower later, and produce more cormlets and contractile roots than do "small" plants.

Such characteristics as large size, late flowering and efficient vegetative reproduction are often associated with polyploidy (Stebbins, 1971), and this relationship was found to be true in *B. douglasii* also. The "small" plant characteristics typically occur in diploid plants, the "robust" characteristics in polyploid plants. It was not possible to distinguish between plants at different polyploid levels by any of the characters used in this study.

The observed characteristics, particularly the size characteristics, are subject to environmental modification. Consequently, size alone is not a very reliable means of determining whether a plant is diploid or polyploid. The number of cormlets produced or the ratio of flowering to non-flowering plants in a population is a better indicator of the ploidy class (diploid or polyploid) of a population. No diploid population was found in which there was an abundance of cormlets, nor was a polyploid population found which did not produce them in abundance.

The greater ability of polyploid plants to reproduce vegetatively and to develop contractile roots results in an ecological separation of polyploid and diploid populations. Polyploid populations are almost always found on steep hillsides, roadbanks, and other sites where the soil is unstable. Seeds would be easily washed away from such sites but cormlets, which start to form a contractile root while still attached to their parent corm, enjoy a much better chance of becoming established. Diploid populations usually occur in rather flat areas or where there is a high density of other plants. Contractile roots are less important in such areas; indeed, many diploid corms are located in the top three inches of the soil. The shorter growth period of diploids results in their flowering one to three weeks earlier than the majority of the other plants in the area. This fact may be significant in reducing competition for the available nutrients.

The ecological separation of diploid and polyploid populations tends to enhance the morphological differences between them. Consequently, when diploid plants from stable sites with dense vegetation are compared with polyploid plants from unstable sites having sparse vegetation, the differences between them are very striking. In Asotin County, Washington, there are a number of localities adjacent to State Highway 129 where the two types of habitat come into contact and even alternate across the landscape. Many of these localities support morphologically distinct diploid and polyploid populations which appear to be completely sympatric. Close examination usually reveals the ecological separation of the two forms.

Polyploidy is common throughout the genus *Brodiaea (senus lato),* but it has not generally been investigated in relation to intraspecific variation. Keator's study (1968) of *Dichelostemma capitatum* Wood (=*B. capitata* Bentham) is a notable exception. His work indicates that the variation within *B. capitata* is very similar in nature to that observed in *B. douglasii.* Moreover, polyploid plants of *B. capitata* tend to have somewhat larger organs than do diploid plants. As in *B. douglasii,* the range of variation of the polyploids overlaps that of the diploids and environmental factors substantially influence the ultimate size of the various plant parts. Keator concluded that most of the observed variation is attributable to environmental rather than genetic factors.

Niehaus (1971) recognized two subspecies in *B. terrestris* Kellogg of which subspecies *kernensis* (Hoover) Niehaus has $n = 24$ and subspecies *terrestris* $n = 6$, 18. The two subspecies are distinguished by the number of vascular strands in the inner perianth segments, but plants of subspecies *kernensis* also tend to be larger than those of subspecies *terrestris* according to Niehaus' descriptions of the two. The two taxa have distinct ranges, subspecies *terrestris* being more northern and coastal than subspecies *kernensis*.

The situation is different in *B. douglasii* in which the diploids and poplyploids have similar distributions, although they usually occupy different habitats. This difference suggests that polyploidy has arisen independently several times within the species. Moreover, the great morphological similarity between diploids and polyploids suggests that the polyploids have arisen through autopolyploidy. This interpretation is supported by the formation of multivalents and other irregularities in polyploid cells. The recognition of infraspecific taxa in *B. douglasii* is not merited on the basis of the characters examined in this study.

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# Double Captures of Four Rodent Species in Oregon

**Abstract**

Possible factors involved in the capture of two animals simultaneously are discussed relative to four species of rodents.

Occurrence of two animals simultaneously in a Sherman live-trap (double capture) has been described by relatively few investigators (Sheppe, 1967; Dunaway, 1968; Petersen, 1975). Getz (1961, 1972), using traps specifically designed for multiple captures, related multiple captures to levels of antagonistic behavior, associated with density, in a population of meadow voles *(Microtus pennsylvanicus)*. This paper suggests possible factors responsible for 51 double captures, involving 80 animals, which occurred during 28,743 trap-nights over a 3-year period on Malheur National Wildlife Refuge, Harney County, Oregon.

Double captures occurred on nine 1.13 ha sites located in desert shrub, marsh and grassland areas, where Sherman live-traps were arranged in square grids ($7 \times 7 = 49$ traps) with 15.0 m intervals between stations. Traps were baited with rolled oats, checked once daily, and were removed following a 10-day trapping period. Rodents comprising double captures included the deer mouse *(Peromyscus maniculatus);* the pocket mouse *(Perognathus parvus);* the western harvest mouse *(Reithrodontomys megalotis);* and the montane vole *(Microtus montanus)*.

Only three instances of interspecific double captures were noted. All involved a *Peromyscus* and a *Perognathus* and in each instance the pocket mouse was killed with no apparent adverse effect to the deer mouse. Evans and Holdenreid (1943) reported similar findings for 27 double captures between species of these genera in California.

Considering conspecific double captures (Table 1), heterosexual pairs occurred more often than homosexual pairs for all species except the montane vole, although only for the harvest mouse was this difference statistically significant (all significance levels were considered to be $P \leq .05$). Petersen (1975) reported finding only heterosexual pairs in 12 double captures of Western harvest mice and Dunaway (1968) trapped only heterosexual pairs of Eastern harvest mice *(R. humulis)*. In the 16 double captures involving voles, only two pairs were heterosexual (Table 1), and of the 14 remaining pairs, all were males.

A double capture suggests that either the pair entered the trap together or that the animals entered separately, but the weight of the initial animal was insufficient to activate the trap. In this study, the average weight of the lightest member of each pair of harvest mice comprising a double capture ($\overline{X} = 9.6$ g.) was not significantly different from the average weight of harvest mice captured alone ($\overline{X} = 10.9$ g., $t = 1.19$, 25 degrees of freedom (df)). However, the average weight of the lightest member of each pair of deer mice comprising a double capture ($\overline{X} = 17.3$ g.) *was* significantly

TABLE 1. Conspecific pairs of rodents comprising double captures during a 3-year period on Malheur National Wildlife Refuge. Chi-square values determine the significance of the number of homo-vs. heterosexual pairs of each species comprising double captures.[a]

| Species | Number of Double Captures ♂♂ | ♂♀ | ♀♀ | Total | $X^2$ value |
|---|---|---|---|---|---|
| *Microtus montanus* | 14 | 2 | 0 | 16 | 6.19[b] |
| *Peromyscus maniculatus* | 6 | 10 | 0 | 16 | 1.64 |
| *Reithrodontomys megalotis* | 0 | 6 | 0 | 6 | 6.00[b] |
| *Perognathus parvus* | 0 | 3 | 1 | 4 | 1.29 |
| Total | 20 | 21 | 1 | 42[c] | |

[a] Trap revealed sex ratios for all species except *R. megalotis* were significantly biased towards males. Thus, the expected values involved in these calculations were appropriately adjusted. Males per 100 females: *M. montanus* = 215; *P. maniculatus* = 173; *P. parvus* = 170.
[b] Significant at $p \leq .05$.
[c] Sex could not be determined on one of the animals in six conspecific double captures.

less than the average weight of deer mice captured alone ($\overline{X} = 20.3$ g., $t = 1.73$, df $= 80$). Of 14 double captures of deer mice in British Columbia, Sheppe (1967) reported that 13 involved two juveniles and the remaining capture a juvenile and an adult.

There was also a significant difference in the average weights of all voles comprising double captures as opposed to those taken alone. These data were then analyzed on a seasonal basis and apparently those double captures which occurred in July 1974 contained animals significantly lighter ($\overline{X} = 19.3$ g.) than the average weight of voles captured alone during this period ($\overline{X} = 37.0$ g., $t = 3.97$, df $= 58$). However, voles comprising double captures during August 1973 or October 1974 presumably entered the traps together, because the average weight of the lightest member of each pair ($\overline{X} = 28.8$ g.) did not differ statistically from the average weight of voles captured alone during these periods ($\overline{X} = 33.5$ g., $t = 1.09$, df $= 54$).

These results suggest that more than one factor probably was responsible for double captures of rodents. The degree of sociability (Getz, 1961, 1972; Petersen, 1975) undoubtedly is a factor, and my data indicate that juvenile male montane voles may forage or disperse together during late summer and fall, as may heterosexual pairs of Western harvest mice. At other times or considering other species, however, the light weight of individual (juvenile) animals and the lack of sensitivity of the trigger mechanism of traps must also be considered as a causative factor of double captures.

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# Effects of Reservoir Formation on the Annual Growth Rings of *Artemisia tridentata*

**Abstract**

This study investigated whether annual growth rings of big sagebrush *(Artemisia tridentata)* bordering Wanapum Reservoir in eastern Washington reflected a change associated with the formation of the reservoir in 1963. There is evidence that the growth of big sagebrush within 2 m elevation above the highwater level of the reservoir was modified.

## Introduction

The effect of reservoirs on surrounding vegetation has not been well studied. In the last 20 years, large irrigation, hydroelectric, and holding reservoirs have been built in the arid regions of eastern Washington, providing a seemingly excellent opportunity for such research.

The native vegetation of this area is largely a shrub steppe; big sagebrush (*Artemisia tridentata* Nutt.) is the main component of this association (Daubenmire, 1970). Recent dendrochronological investigations have indicated that big sagebrush reflects changes in moisture status by variations in the width of the xylem layers in the stem. Ferguson (1964) found a correlation between the xylem layers of big sagebrush and winter precipitation. Daubenmire (1975) reported that xylem layer growth in big sagebrush is closely related to November through June precipitation and to soil moisture in May. Fowler and Helvey (1974) detected a growth response of big sagebrush to irrigation, as well as a correlation between variation in xylem layer growth and August through July precipitation.

The objective of the present study was to determine any changes in the annual growth rings of big sagebrush that might be associated with the 1963 establishment of Wanapum Reservoir in Grant County, Washington. The hypothesis was that the formation of the reservoir resulted in an improved water regime for big sagebrush in the immediate vicinity of the reservoir which would be reflected in the annual growth rings.

## Methods and Materials

The reservoir site was selected according to three criteria. These were that big sagebrush extend to the highwater level, that there be a gradual elevational gradient away from the reservoir, and that there be no visible fire, construction, or recreational disturbance. Four plots (1-4) adjacent to the reservoir were established at this site.

A control site (plot 5) was established approximately 100 m above the reservoir on a plateau about 2 km away from the reservoir site. Another site (plot 6) that had burned in July 1967 was established about 11 km west of Quincy, Washington. It was anticipated that this plot would provide information on the response of big sagebrush to fire, a common range practice in shrub steppe areas (Pechanec, 1944).

Selection of big sagebrush specimens was based on the condition of the stem and the elevation and distance of the plant from the reservoir highwater level. Many specimens were too decayed or too young to be used for analysis. Approximately 30 years of growth rings were required so as to avoid using the potentially anomalous rings near the pith (Duff and Nolan, 1953) and yet allow 10 years pre- and post-1963 for the statistical tests.

Big sagebrush specimens from all six plots were prepared and crossdated by standard dendrochronological techniques as described by Ferguson (1964) and Stokes and Smiley (1968). Ring widths were measured to .01 mm on an incremental measuring apparatus. A Fortran program developed by Harold Blair of the College of Forest Resources, University of Washington, was utilized to check the crossdating. Crossdating facilitated the assignment of a year date to each ring.

#### Results and Discussion

Fifty-two (of 78) big sagebrush plants collected were appropriate for analysis. The ring widths of each specimen were graphed against year of formation. Plot composites were prepared by averaging the ring widths for each year (Fig. 1). An analysis of variance was run on the data for each plot. It indicated that the variation due to years was significantly (P=.02) greater than the variation due to individuals for all plots except plot 2. With the exception of plot 2, the composite graphs therefore indicate ring width variations are due to years; they are not unduly influenced by unusually erratic specimens.

Plot 1 exhibits a dramatic increase in ring width in 1961; plots 3 and 4 exhibit a similar increase in 1956. These increases tended to be sustained in plots 2 and 5. Plots 1-5 exhibit a decrease in ring width in 1955, followed by a large increase in 1956. The ring width fluctuations of plot 6 (fire site) do not correspond with any of the dramatic fluctuations exhibited on the other plots. Plots 2 and 3 exhibit a large ring width fluctuation in 1964, the first growing season after reservoir formation.

Since the main purpose of this study was to determine if there is a relationship between the formation of Wanapum Reservoir and a growth response in big sagebrush, the next step was to test if the mean ring width for the 10 annual growth rings previous to reservoir formation (1953-1962) was significantly different from that for the 10 years (1964-1973) after reservoir formation. T-tests (Campbell, 1974) were run to compare these pre- and post-10 year segments for each individual plant. If the post-1963 segment was significantly greater at the P=.05 level than the pre-1963 segment, a +S was assigned that segment; if it was significantly less, a –S was assigned (Table 1).

When the reservoir site (plots 1-4) is compared with the control and fire sites, approximately 20 percent of the individual plants within each site exhibit a significant

TABLE 1. Results of t-tests (in percent) for radial segments for 10 years pre- and post-1963 (P=.05).

| Site | n | Length Differences Significance | |
|---|---|---|---|
| | | %+S | %–S |
| Reservoir | 33 | 18 | 6 |
| Control | 10 | 20 | 20 |
| Fire | 9 | 22 | 22 |

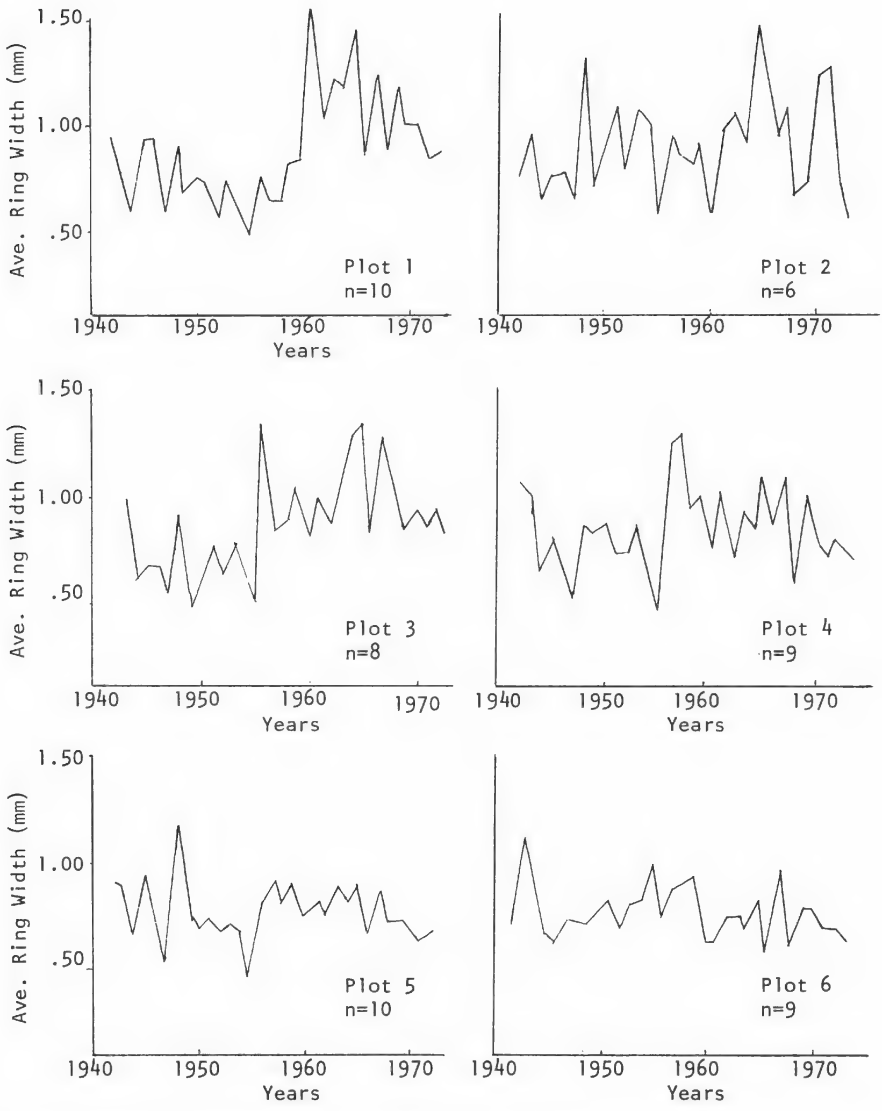


Figure 1. Composite site graphs of yearly ring width fluctuations.

increase in the radial segment length after reservoir formation. However, only 6 percent of the plants on the reservoir plots exhibited a significant decrease in the radial segment length after reservoir formation, while on the control and fire sites 20 percent and 22 percent respectively exhibited a decrease (Fig. 2).

These data (Fig. 2) seem to indicate a mitigating influence of the reservoir for plants whose growth is marginal or decreasing relative to the growth of the other plants. It also seems to indicate that the 1967 fire at plot 6 did not retard or enhance the growth

of the surviving plants based on the similarity of the changes in the radial segment length of the control and fire sites.

The postulated mitigating influence of the reservoir and the extent of the hypothesized reservoir effect were further investigated. Meredith (1965) developed a graph to indicate the extent of reservoir influence on adjacent ponderosa pine. Figure 3 shows similar data for big sagebrush. The length of the 10 year pre-1963 segment is subtracted from the length of the 10 year post-1963 segment. This difference is graphed against elevation. Individual specimens are labeled with their identification numbers. Figure 3 shows a dramatic drop in the growth differences at 2 to 2.5 m in elevation above the reservoir highwater level. This elevation could be interpreted as the extent of reservoir influence on big sagebrush.

To substantiate further the extent of reservoir influence on big sagebrush, elevational groups were delineated. The results of the t-tests for each specimen were placed within each group; however, the results were inconclusive.

Meredith (1965) found that the differences in annual growth ring variance for pre- and post-reservoir segments were more distinctive than the differences in the length of the pre- and post-reservoir segments. The annual growth ring variance of the 10 year pre- and post-1963 segments of big sagebrush was analyzed using an F-test (Campbell, 1974). Table 2 contains the results of the t-tests and the F-tests at 0-2 m and >2 m elevation. It also has a summary of the F-tests at all three sites.

Although the t-tests indicate no difference in 10 year segment length with proximity to the reservoir, the F-tests indicate that plants less than 2 m in elevation above the reservoir significantly increase their annual growth ring variation, while those >2 m in elevation significantly decrease their annual growth ring variation. Meredith (1965) found the same trend in variance with ponderosa pine. A comparison of the three sites without the elevational gradient masks this difference.

#### Conclusions

T-tests performed on the length of big sagebrush radial segments for the 10 years pre- and post-reservoir formation indicated a mitigating influence of the reservoir on the plants on the reservoir plots. The mechanism for the observed difference in the plants exhibiting a significant decrease in radial growth was unclear, as elevation groupings at the reservoir plots did not correlate with this decrease. However, only 6 percent of the plants at the reservoir site exhibited a decrease in radial growth while 20 percent of the plants at the control site exhibited this decrease.

TABLE 2. Results of statistical tests (in percent) for radial segments for 10 years pre- and post-1963 (P=.05).

| Test | Site | Elevation in m | n | Significance %+S | %−S |
|---|---|---|---|---|---|
| t-test | Reservoir | 0-2 | 18 | 17 | 6 |
| | Reservoir | 2 | 15 | 20 | 7 |
| F-test | Reservoir | 0-2 | 18 | 22 | — |
| | Reservoir | 2 | 15 | — | 20 |
| F-test | Reservoir | | 33 | 12 | 9 |
| | Control | | 10 | 10 | 10 |
| | Fire | | 9 | — | — |

F-tests performed on the same big sagebrush segments indicated that all the significant increases in annual growth ring variation (22 percent) occurred 0-2 m in elevation above the reservoir highwater level while all the significant decreases in annual growth ring variation (20 percent) occurred at >2 m in elevation. This difference in

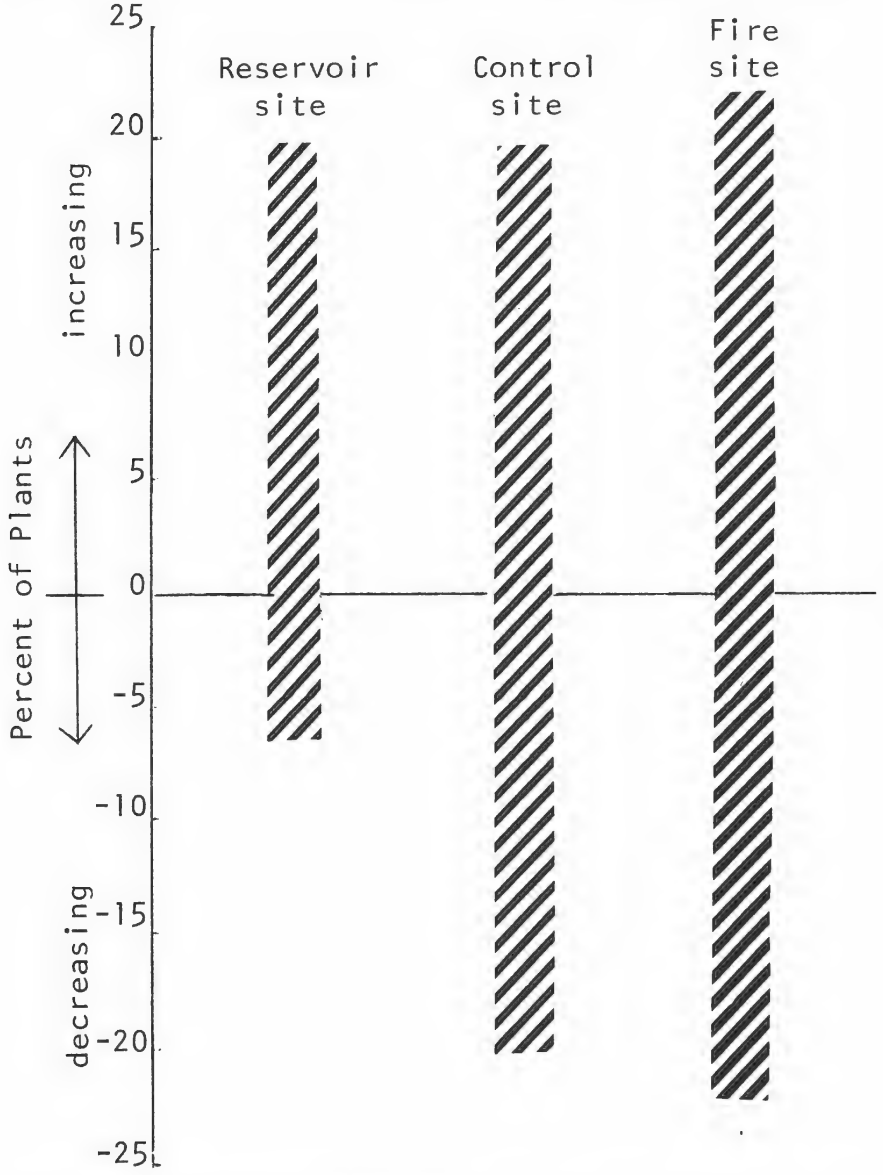


Figure 2. Percent of plants exhibiting a significant increase or decrease in radial segment length after 1963.

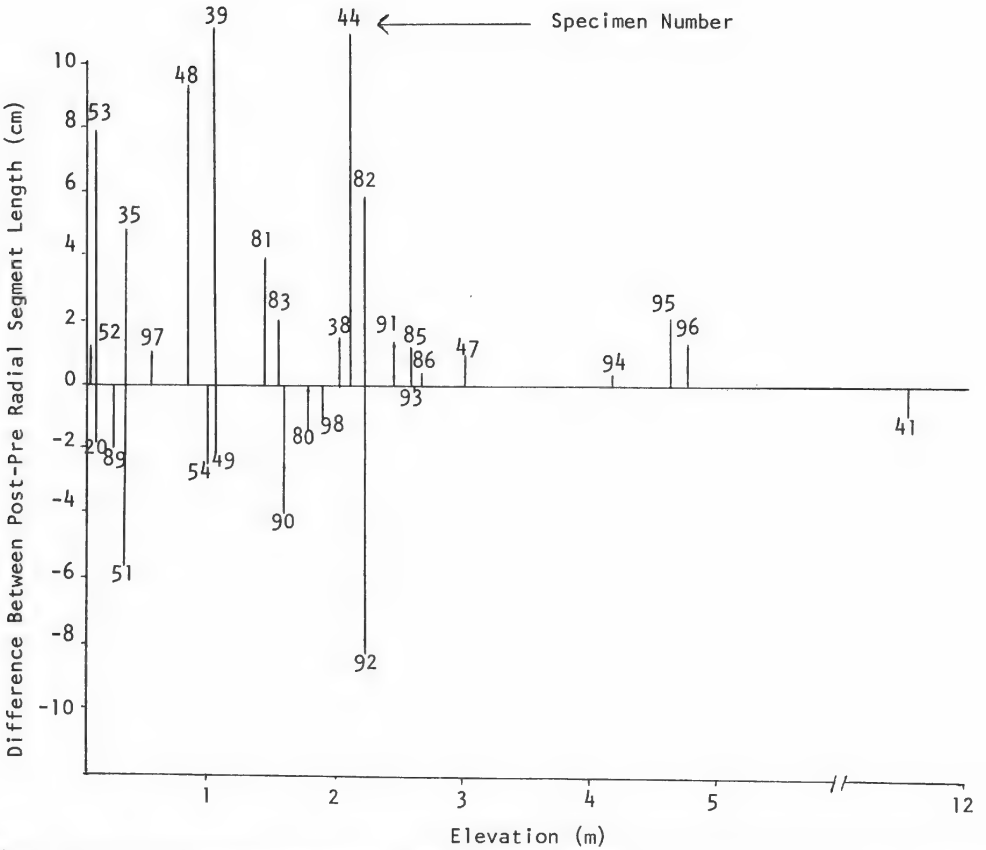


Figure 3. Relationship between elevation and post-1963 radial segment length minus pre-1963 radial segment length.

variance due to elevational gradient was masked when the reservoir site (without elevational groupings) was compared with the control site.

A graph representing the increase or decrease of the 10 year segment length post-reservoir over that of the pre-reservoir segment indicated that the extent of reservoir influence was 2 to 2.5 m.

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# Habitat Utilization and Resource Partitioning by Wild Ruminants: Multivariate Analysis of Nominally-Scaled Attribute Data

**Abstract**

Multivariate nominal scale analysis, a relatively new statistical technique, was applied to the study of habitat use and resource partitioning in a western Canadian native grazing system comprised of whitetailed deer, mule deer, wapiti and bighorn sheep. Even when these species were concentrated on restricted winter/spring ranges, a degree of ecological separation was detected with each species showing distinct preferences for different habitats. The statistical technique applied offered a number of advantages for handling ecological data of this type.

## Introduction

The relatively high biomass and productivity of multi-species grazing systems has been attributed to more balanced and complete utilization of vegetation resources by the various members of the assemblage (Talbot, 1966). The manner in which these animals partition resources and hence coexist has only recently been subjected to careful quantitative analyses (Bell, 1971; Ferrar and Walker, 1973; Harris, 1973). Generally, these studies have revealed that functional interactions within grazing communities are surprisingly complex and subtle. Nevertheless, it would appear safe to generalize that niche differentiation among co-existing herbivores most commonly involves separation along the dimensions of habitat (space), food, and time. Of these, the habitat dimension perhaps is of greatest importance for large primary consumers (Schoener, 1974), particularly in the topographically complex rangelands of Western North America.

One of the major problems facing analysis of occupational patterns and spatial overlap is that of uncovering the vectorial response of animals to various habitat parameters. In such investigations there are a number of questions that can be posed. How well do habitat variables as a whole explain variation in areal distribution? In other words, how selective are animals? What is the marginal usefulness of any particular habitat attribute in increasing the predictability of habitat use patterns? Once an appropriate statistical model has been fit, further questions can be asked regarding its predictive power. For example, given scores of any location on a number of attributes, what is the likelihood that a given species would be present? By how much do actual occupational patterns deviate from those predicted?

In this study, an attempt is made to answer these questions using a relatively new statistical technique termed multivariate nominal scale analysis (Andrews and Messenger, 1973). The procedure is illustrated with an analysis of spatial relationships and resource partitioning by whitetailed deer, mule deer, wapiti, and bighorn sheep in a Western Canadian native grazing system.

## Methods and Materials

### *1. Study Area*

The data used to illustrate the statistical method were collected as part of a study con-

ducted on Premier Ridge, an important wildlife winter/spring range located in the Rocky Mountain Trench of south eastern British Columbia. A detailed description of the study area is provided in reports by Kemper (1972) and Hudson *et al.* (1976). Briefly, Premier Ridge rises approximately 550 m above the floor of the Kootenay River Valley on the western slope of the Rocky Mountains. The original plant community was a mixed montane forest of ponderosa pine *(Pinus ponderosa)* and Douglas-fir *(Pseudotsuga menziesii),* although this was disturbed by fire and logging in the early part of this century. Grasslands now exist on dry benches and slopes of south to west exposure whereas lodgepole pine *(Pinus contorta)* dominates the base and lower slopes of the ridge. Bluebunch wheatgrass *(Agropyron spicatum)* and rough fescue *(Festuca scabrella)* are dominant except in heavily grazed areas where blue grasses (*Poa* spp) and needle grasses (*Stipa* spp) have replaced the climax species.

Premier Ridge presently supports healthy populations of whitetailed deer *(Odocoileus virginianus),* mule deer *(Odocoileus hemionus),* wapiti *(Cervus canadensis)* and Rocky Mountain bighorn sheep *(Ovis canadensis).* These species generally utilize the area from about November to April depending upon annual sequences of plant phenology and snowfall.

*2. Data Set*

Occupational patterns of each of the represented large ruminant species were assessed by direct observation along predetermined census routes traversed on foot, skiis, or by vehicle. At each sighting a profile of 15 habitat attributes was recorded on prepared observation forms (Table 1).

*3. Analytical Methods*

Partitioning of habitat resources was analyzed by comparing the vectorial responses of the four major native ruminants. For this purpose observations were stratified into winter (November 1-March 13) and spring (March 14-April 15) periods. Only observations of animals which were actively foraging were included since this was assumed to be more relevant to resource division. Sightings were weighted according to the size of the group present.

Two statistics were calculated to measure the multivariate strength of association, that is, to answer the question of how well habitat variables as a whole explained observed patterns of spatial distribution. These were the generalized multiple regression coefficient *(R-squared)* and the multivariate *Theta* statistic. The generalized *R-squared* was calculated as the ratio of total explained sum of squares to total sum of squares. The multivariate *Theta* statistic was determined as the proportion of cases correctly classified *a postiori* following categorical assignment on the basis of the highest probability of inclusion.

The strength of the bivariate relationship between the dependent variable (species) and each habitat attribute was measured using the one-way analysis of variance *Eta-squared* coefficient which measured explained variance and the bivariate *Theta* statistic which used the criterion of correct assignment to the dependent variable categories. An experimental statistic, *Beta-squared,* was calculated to explore the unique predictive power of different independent variables while controlling for all others. It was roughly analogous to the partial regression coefficient of conventional multiple regression analysis

TABLE 1. Observational data collected for each animal sighting

| Variable type | Variable name | Categories | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Dependent variable | Species | Whitetail deer | mule deer | elk | bighorn sheep | —— | —— | —— | —— |
| Stratification variable | Weather | clear, warm | windy | cold | snow/rain | —— | —— | —— | —— |
| " | Date | Nov 1-Dec 31 | Jan 1-Feb 1 | Feb 1-Mar 13 | Mar 15-May 29 | Mar 30-Apr 15 | —— | —— | —— |
| " | Time | Dawn-mid morning | late morning | Early afternoon | late afternoon | —— | —— | —— | —— |
| " | Activity | resting | grazing | fleeing | casual movement | —— | —— | —— | —— |
| Predictors (independent variables) | Slope (percent) | 0-5 | 6-10 | 11-20 | 21-40 | 41 + | —— | —— | —— |
| " | Aspect | north | north-east | east | south east | south | south-west | west | north-west |
| " | Terrain | slope | rock outcrop | bench | swale | ridge | —— | —— | —— |
| " | Vegetation-structure | open timber | shrub | grass | complex | —— | —— | —— | —— |
| " | Major tree species | fir | ponderosa pine | lodgepole pine | mixed conifer/decid. | aspen | birch | —— | —— |
| " | Major shrub species | bitterbrush | buffalo berry | saskatoon | mixed | —— | —— | —— | —— |
| " | Major grass species | *Agropyron/ Festuca* | *Poa* | *Stipa* | *Calamagrostis* | mixed | —— | —— | —— |
| " | Snow depth (inches) | 0 | 1-2 | 3-4 | 5-8 | 9 + | —— | —— | —— |
| " | Snow cover (percent) | 0-10 | 11-50 | 51-75 | 76-95 | 96-100 | —— | —— | —— |
| " | Snow hardness (increasing) | score 1 | score 2 | score 3 | score 4 | score 5 | —— | —— | —— |

except that it had the somewhat inconvenient property of being specific to a particular category of dependent variable rather than being generalized to all categories.

Predictions of probabilities that given sightings would involve a particular species were computed by summing the relevant coefficients separately for each species and adding this sum to the overall percentage representation of that species. Once a set of predicted scores was calculated for each location, the case was assigned to the species for which the probability was highest. Such predicted assignments were compared with those actually observed in order to test the performance of the statistical model. All calculations were performed using MNA, an OSIRIS III library program (University of Michigan, 1973).

**Results**

*1. Performance of the Complete Model*

The strength of the relationship between spatial abundance of each species and environmental attributes taken together was revealed by two statistical parameters (Table 2). The generalized *R-squared* indicated that the complete model accounted for 23 (winter) to 25 (spring) percent of variance in the species-specific patterns of distribution. Values of multivariate *Theta* for winter and spring periods were .58 and .59 respectively, indicating that over 58 percent of sightings could be correctly allocated to one of the species after taking into account the environmental attributes of each location. These values were compared with the percentage occurrence of the modal species category (in this case, whitetailed deer at approximately 35 percent), since even if nothing were known about the environment, predictions that each animal sighting would involve this species would be correct 35 percent of the time. Hence, the complete model increased predictability approximately 23 percentage points.

When the model was applied in predictive mode to evaluate *a postiori* probabilities of species' presence or absence according to the profile of attributes shown by various locations, a pattern of correct assignments reflective of ecological dissimilarity of each species pair was obtained (Table 3). In both seasons, whitetailed deer and mule deer were most distinctive in their habitat preferences. Wapiti overlapped mule deer and whitetailed deer to a degree. Bighorn sheep habitat preferenda coincided with those of mule deer.

*2. Variable-Specific Summary Relationships*

Of 10 predictor variables included in the study, only major grass species, major shrub species, major tree species, terrain, and vegetation structure appeared important in segregation of the four ruminants. Inspection of generalized *Eta-squared* values showed that each of these variables accounted for between 2 and 8 percent of the variation. Examination of bivariate *Theta* values showed that, taken individually, each predictor resulted in only marginal increases in predictive power, the highest increasing the probability of correct prediction from 35 percent to 45 percent.

The unique contribution of each environmental predictor was different for each species. This fact was evident in the relative magnitude of *Beta-squared* values for each species (Table 2). For whitetailed deer, major grass species followed by major shrub species were the prime determinants of distribution. Mule deer were most strongly influenced by shrubs, wapiti by tree cover, and bighorn sheep by grasses and terrain.

TABLE 2. Resource partitioning: summary statistics and evaluation of five major predictors.

| | Winter | | | | | Spring | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Overall | White deer | Mule deer | Elk | Bighorn sheep | Overall | Whitetail deer | Mule deer | Elk | Bighorn sheep |
| *Multiple Relationships* | | | | | | | | | | |
| Complete model | | | | | | | | | | |
| Percentage distribution | | 35.97 | 31.30 | 23.95 | 8.78 | | 35.07 | 27.73 | 26.82 | 10.38 |
| Generalized R**2 | 0.2323 | | | | | 0.2517 | | | | |
| Multivariate Theta | 0.5800 | | | | | 0.5939 | | | | |
| Adjusted R**2 | | 0.2817 | 0.1602 | 0.1662 | 0.1770 | | 0.3418 | 0.1188 | 0.1300 | 0.1763 |
| *Major Grass Species* | | | | | | | | | | |
| Generalized Eta**2 | 0.0767 | | | | | 0.0862 | | | | |
| Bivariate Theta | 0.4541 | | | | | 0.4369 | | | | |
| Eta**2 | | 0.1517 | 0.0642 | 0.0124 | 0.0403 | | 0.1945 | 0.0470 | 0.0218 | 0.0413 |
| **Beta**2** | | 0.1445 | 0.0194 | 0.0349 | 0.0676 | | 0.1728 | 0.0185 | 0.0411 | 0.0778 |
| *Major Shrub Species* | | | | | | | | | | |
| Generalized Eta**2 | 0.0574 | | | | | 0.0578 | | | | |
| Bivariate Theta | 0.4426 | | | | | 0.4343 | | | | |
| Eta**2 | | 0.1004 | 0.0618 | 0.0216 | 0.0037 | | 0.1149 | 0.0288 | 0.0476 | 0.0019 |
| Beta**2 | | 0.0692 | 0.0574 | 0.0245 | 0.0365 | | 0.0580 | 0.0226 | 0.0311 | 0.0397 |
| *Major Tree Species* | | | | | | | | | | |
| Generalized Eta**2 | 0.0494 | | | | | 0.0500 | | | | |
| Bivariate Theta | 0.3925 | | | | | 0.3720 | | | | |
| Eta**2 | | 0.0725 | 0.0389 | 0.0458 | 0.0196 | | 0.0745 | 0.0363 | 0.0466 | 0.0263 |
| Beta**2 | | 0.0536 | 0.0376 | 0.0446 | 0.0053 | | 0.0441 | 0.0307 | 0.0301 | 0.0155 |
| *Terrain* | | | | | | | | | | |
| Generalized Eta**2 | 0.0507 | | | | | 0.0515 | | | | |
| Bivariate Theta | 0.4114 | | | | | 0.3906 | | | | |
| Eta**2 | | 0.0466 | 0.0655 | 0.0190 | 0.0951 | | 0.0611 | 0.0628 | 0.0223 | 0.0656 |
| Beta**2 | | 0.0195 | 0.0482 | 0.0237 | 0.0457 | | 0.0326 | 0.0468 | 0.0192 | 0.0173 |
| *Vegetation Structure* | | | | | | | | | | |
| Generalized Eta**2 | 0.0211 | | | | | 0.0307 | | | | |
| Bivariate Theta | 0.3687 | | | | | 0.3651 | | | | |
| Eta**2 | | 0.0122 | 0.0045 | 0.0227 | 0.0880 | | 0.0180 | 0.0069 | 0.0363 | 0.1009 |
| Beta**2 | | 0.0049 | 0.0186 | 0.0229 | 0.0425 | | 0.0088 | 0.0212 | 0.0270 | 0.0572 |

*3. Variable-Specific Response Profiles*

Coefficients of the MNA model, which illustrate the effects of various environmental attributes on the likelihood of a particular species being involved in any sighting, are displayed in Table 4. These coefficients account for any relationships that may have been present among the various environmental variables and between each environmental variable and each species. Thus, they can be interpreted directly as the gain or loss in likelihood after statistically controlling all other predictors.

The pattern of coefficients found in this study can be interpreted as follows. The greatest likelihood of winter whitetailed deer sightings occurred in shrub communities on benches or swales where mixed grass or *Stipa* species were predominant and where

TABLE 3. Classification matrix—*a postiori* assignment (percent).

| Actual | Predicted | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Winter | | | | Spring | | | |
| | Whitetail deer | Mule deer | Elk | Bighorn sheep | Whitetail deer | Mule deer | Elk | Bighorn sheep |
| Whitetailed deer | 73.20 | 22.12 | 3.53 | 1.14 | 77.54 | 16.08 | 5.31 | 1.06 |
| Mule deer | 17.30 | 72.87 | 7.99 | 1.85 | 17.66 | 66.22 | 12.28 | 3.84 |
| Elk | 30.48 | 41.10 | 26.20 | 2.23 | 24.01 | 34.13 | 38.69 | 3.17 |
| Bighorn sheep | 14.49 | 42.99 | 13.08 | 29.44 | 8.72 | 44.62 | 13.33 | 33.33 |

TABLE 4. Response profiles: coefficients of MNA model.

| Predictor variable and levels | Winter | | | | Spring | | | |
|---|---|---|---|---|---|---|---|---|
| | Whitetail deer | Mule deer | Elk | Bighorn sheep | Whitetail deer | Mule deer | Elk | Bighorn sheep |
| *Major Grass Species* | | | | | | | | |
| *Agropyron-Festuca* | -25.78 | 6.46 | 14.44 | 4.89 | -27.33 | 3.39 | 17.53 | 6.41 |
| *Poa* spp | -2.71 | 1.82 | -3.16 | 4.05 | -5.15 | 4.08 | -3.37 | 4.44 |
| *Stipa* spp | 56.93 | -9.22 | -22.12 | -25.59 | 57.08 | -5.87 | -22.25 | -28.97 |
| *Calamagrostis* | 6.83 | 3.11 | -4.55 | -5.38 | 6.77 | -4.07 | -0.15 | -2.20 |
| Mixed | 75.24 | -28.92 | -38.74 | -7.58 | 65.00 | -21.72 | -32.08 | -11.93 |
| *Major Shrub Species* | | | | | | | | |
| *Purshia* | 9.01 | 2.99 | -7.07 | -4.94 | 10.04 | 2.03 | -6.39 | -5.67 |
| *Shepherdia* | -26.68 | 19.21 | 10.08 | -2.61 | -21.99 | 11.00 | 15.31 | -4.32 |
| *Amelanchier-Prunus* | -12.38 | 19.08 | -7.46 | 0.76 | Not represented in spring sample | | | |
| Mixed | -0.60 | -15.94 | 14.86 | 1.68 | -11.80 | 9.67 | 0.48 | 1.65 |
| *Major Tree Species* | | | | | | | | |
| *Pseudotsuga* | 7.64 | 0.41 | -5.94 | -2.11 | 4.63 | 2.26 | -1.82 | -5.07 |
| *Pinus ponderosa* | -29.88 | -37.98 | 70.57 | -2.72 | -15.51 | -42.87 | 60.90 | -2.52 |
| *Pinus contorta* | 28.47 | -20.22 | -4.34 | -3.91 | 28.25 | -17.85 | -3.77 | -6.63 |
| *Populus* | -8.43 | 32.93 | -18.41 | -6.10 | 6.27 | 16.60 | -8.78 | -14.09 |
| Mixed | -2.67 | -27.73 | 35.91 | -5.51 | -25.80 | -25.68 | 55.53 | -4.06 |
| *Terrain* | | | | | | | | |
| Slope | -1.99 | 4.88 | -1.46 | -1.43 | -2.98 | 4.92 | -1.29 | -0.66 |
| Rock outcrop | 2.14 | -9.46 | -17.33 | 24.65 | 7.65 | -4.88 | -16.94 | 14.18 |
| Bench | 12.24 | -18.16 | 8.13 | -2.22 | 16.39 | -20.49 | 7.41 | -3.31 |
| Swale | 11.02 | -3.30 | -13.22 | 5.50 | -6.53 | 3.90 | -6.18 | 8.82 |
| Ridge | -32.48 | 63.88 | -20.79 | -10.61 | -33.66 | 49.77 | -9.48 | -6.63 |
| *Vegetation Structure* | | | | | | | | |
| Open timber | -2.68 | 8.36 | -1.83 | -3.85 | 0.19 | 10.92 | -6.59 | -4.52 |
| Shrubland | 3.66 | -6.29 | 2.58 | 0.06 | 1.53 | -5.60 | 3.87 | 0.20 |
| Grassland | -5.63 | 2.98 | -14.45 | 17.09 | -9.06 | -2.13 | -9.08 | 20.26 |
| Mosaic | -2.22 | -1.21 | 7.58 | -4.15 | -2.46 | 0.65 | 8.06 | -6.26 |

bitter-brush *(Purshia)* and lodgepole pine were the most important associated shrub and tree species. During spring the pattern was similar except that swales were avoided and rock outcrop habitats were more commonly used.

The greatest likelihood of sighting mule deer in winter was on open timbered ridges supporting an overstory of aspen or Douglas-fir and a shrub layer comprised of buffalo berry *(Shepherdia)* or saskatoon *(Amelanchier)*. Wheat grasses and rough fescue also were important positive determinants of distribution. Major changes in habitat preference associated with the spring flush of vegetation involved increased use of the early greening blue grass communities.

The highest probability of winter sightings of wapiti was on benchlands supporting complex mosaics of vegetation types. Ponderosa pine, mixed shrubs, and wheatgrass-fescue communities were the important vegetation components. Major changes associated with the onset of spring were increased use of mixed forest stands with a stronger representation of buffalo berry.

Bighorn sheep were most predictably sighted during winter in rock outcrop habitats within grassland communities. The presence of wheatgrass, fescue, and blue grass all increased the probability of sighting bighorn sheep. Associated with the spring period were reduced use of rock outcrops and increased use of swales.

**Discussion**

*1. Ecological Interpretation*

The complete model was statistically significant, but predictability was not high as revealed by *R-squared* and multivariate *Theta* values. These measures of the goodness-of-fit described the likelihood that a sighting would involve a given species. Thus, the complete model evaluated species distinctiveness or ecological separation rather than habitat preference directly.

Goodness-of-fit measures reflected two confounding items: (1) the success with which the environment was described in terms relevant to free-ranging animals, and (2) the actual intensity of resource partitioning. In this study, a number of improvements of habitat measurement were indicated. For example, one very important determinant of distribution appeared to be the phenologic stages of forage grasses, particularly the pattern of spring emergence. Areal variation in quality of shrubs and cured forage grasses also may have improved the fit of the statistical model. But in spite of these possible shortcomings, this analysis did demonstrate that even on a restricted winter/spring range, there was a degree of resource partitioning along the habitat dimension. Because of the composition of the error term, this measure of resource partitioning must be considered conservative. In the absence of comparative information from other grazing systems and in the absence of parallel information on the partitioning of complementary resource dimensions, it is difficult to evaluate the degree of separation described. Limiting degrees of ecological similarity in various environments are not known in quantitative terms (May, 1974).

Ecological distances (dissimilarity) for various species pairs are difficult to determine using MNA when all species are not equally abundant. Adjusted R-squared and *a postiori* assignment of cases can provide a general indication. However, methods such as principal coordinate analysis (Blackith and Reyment, 1971) perhaps would give a more convenient display of ecological relationships. Although pair-wise summary meas-

ures are not presented, the major ways in which the herbivore species differed were clear. The major environmental attributes which resulted in these distinctive habitat preferences in general were ecologically interpretable and consistent with studies conducted elsewhere. The importance of grass species and terrain in providing food and escape cover for bighorn sheep and the importance of grass species and timber for elk is well-known (Constan, 1972; Mackie, 1970). The importance of shrubs, the major winter food of mule deer, is also interpretable (Kufeld *et al.,* 1973). Only the importance of grass species in the distribution of whitetailed deer is puzzling upon initial inspection, since grass does not form an important part of the winter diet of this species. However, the mixed-grass communities to which they responded also supported an array of forbs such as kinnikinnik *(Arctostaphylos uva-ursi),* phlox (*Phlox* spp.), and in some locations clover (*Trifolium* spp.), all of which appeared important in the winter diet. The responses of whitetailed deer to these early greening grass communities during spring were consistent with their seasonal forage preferences.

This analysis must be considered only descriptive of occupational patterns of these coexisting native ruminants. Sale (1974) has emphasized that contrary to the usual interpretation, overlap can be used as evidence either for or against the existence of competition. Definitive conclusions regarding functional interaction can only be drawn when it is demonstrated that distributions and habitat preferences are altered in the presence of another species and this change is consequential to productivity.

*2. Evaluation of Statistical Procedures*

There are two general approaches to collection of distributional data when the goal is to evaluate the response of animals to a series of environmental parameters. The more common procedure and the one adopted in this study is to accumulate records of parameters associated with each individual animal sighting. This data set is then contrasted statistically with a similar set intended to be representative of what is available on the study area. A second approach involves stratification of an area on the basis of habitat type (Shannon *et al.,* 1975) or with a systematic grid (Hudson *et al.,* 1976). Cumulative animal sightings are then used directly as the dependent variable or used as a criterion for classification of the area as preferred or not preferred habitat.

Depending upon the manner in which the data is collected, the types of measurement chosen for environmental attributes and other characteristics of the data set, a number of alternative analytical methods and statistical models can be chosen.

Multiple regression and partial correlation are classical techniques when data sets approximate the implicit basic assumptions of interval scale measurement, homoscedasticity and linear additive relationships. These methods are most readily applied to cumulative sightings taken from stratified habitat units or a systematic grid since the dependent variable is expressed as a continuous interval scale. However, it is possible to apply the method to dichotomous present/absent data by scoring these two states (0=absent, 1=present) and interpreting the results as probabilities of occupation. A common practice in application of regression techniques to spatial analysis is to build a statistical model interatively by mapping residuals of regression to determine locations of strong over- and under-estimation. Inspection of these locations often suggests new variables which should be included (Berry and Marble, 1968). Although the technique has been successfully applied in the analysis of animal distribution (Anderson *et al.,* 1972; Shannon *et al.,* 1975; Hudson *et al.,* 1976), the assumptions of the methods often are violated

and many habitat attributes are not conveniently described in interval or ratio scales. Additional problems arise from multicollinearity of independent variables and from the characteristic non-linear unimodel response of animals to habitat attributes (Slobodkin, 1968).

Multiple classification analysis (Andrews *et al.,* 1967) offers an advantage in that relationships between dependent and independent variables need not be linear and independent variables need not be measured as interval scales, although continuous scale measurement of the dependent variable is still assumed and other limitations of multiple regression techniques apply. In spite of the obvious advantages offered, MCA has not been applied widely to analysis of spatial distributions of large mammals.

Multiple discriminant function analysis is a widely applied multivariate technique for analyzing data in which the dependent variable is in nominal form. Although accepting categorical measurement of the dependent variable, the method assumes that all independent variables are measured as interval scales and have linear additive effects. These assumptions are less restrictive than those associated with multiple regression. A further advantage is that since a relatively large number of categories of the dependent variable can be included, the model is appropriate for studying resource division in complex assemblages of species as well as habitat selection through analysis of present/absent dichotomies. Such techniques have been applied by Ferrar and Walker (1973) and Hudson (1976) to the analysis of native grazing systems.

Multivariate nominal scale analysis, the technique used in this study, provides flexibility for handling ecological data where the dependent variable is a set of discrete categories, independent variables are measured at any level of measurement (nominal, ordinal, interval, ratio), and where variable patterns of relationships exist between any independent variable and the dependent variable and among sets of independent variables. One of the few necessary assumptions is that an additive model is appropriate (Andrews and Messenger, 1973). Another more pragmatic advantage is that measurements, since they can be collected in nominal form, often are more meaningful to managers and more easily collected by field workers.

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# A Bibliography on Vegetation of the State of Washington: Supplement I

**Abstract**

This is a supplement to a preliminary listing which appeared in this journal (pp. 50-54) in 1962. The intent has been to include all published literature pertaining to studies of post-Wisconsin macroscopic plant communities in the State of Washington, and their ecology. The previous list included 106 titles, and this supplement adds 86 more.

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# Prey Selection by the Rough Skinned Newt (Taricha granulosa) in Two Pond Types

**Abstract**

The stomach content analyses of the rough skinned newt, *Taricha granulosa,* from a permanent pond indicate a higher degree of prey diversity than found in a sample taken from a temporary pond. There is a highly significant correlation between snout-vent length (SVL) and head width within samples. There are also significant differences in SVL and head width between samples.

## Introduction

The prediction of feeding strategies which might be exhibited by groups of organisms is an active area of interest in population biology. A particular aspect of interest is whether a particular predator may be considered a food generalist or a food specialist, and what environmental or behavioral factors influence this choice of feeding activity (Emlen, 1973). Intuitively one might expect that the prey utilized by a predator would directly reflect the abundance and diversity of prey available. However, most modelers predict that when a predator has an abundant amount of prey available, there will be a tendency towards specialization, and that when resources are limiting, the predators will become generalists in their food selection (Emlen, 1966; Schoener, 1971; Pulliam, 1974). These authors also suggest that when a predator is confronted with a heterogenous environment the generalist will be favored. An essential point concerning these predictions and models is that they are useful if they lend themselves to field or *in vivo* verification (Menge, 1972).

Emlen (1973) has succinctly outlined how specialization might be adopted by a predator. If a wide variety of prey is made available to an animal, the more abundant (here I am equating abundance with ease of capture) will be captured. Presumably, because this prey is eaten more often, the predator will become more efficient in its capture and ingestion. This specialization for a particular prey type would then be maintained as long as the prey was abundant. When the density of prey is reduced the predators will switch to a generalist type of strategy. Menge (1972) was able to verify several of these predictions in his work with the starfish *Leptasterias hexactis.*

The mechanism for this switch has been debated by several authors. Emlen (1973) believed that the predator will initiate selection of an alternate prey when those prey begin to outnumber the preferred prey. Pulliam (1974) believed that the switch is independent of the alternate prey density, and that it is purely a function of the availability of the preferred prey. Schoener (1971) has suggested that the presence or absence of hunger may be the cue for a switch towards generality. In consideration of these ideas we can ask if a predator considered to be a generalist would in fact select a specialist type of feeding strategy under the proper conditions. If one did find differing strategies

being utilized by a particular organism, would there also be a corresponding shift in body size, as suggested by Schoener (1969), who felt that if prey were abundant a large predator would be favored and conversely, if prey were limiting, would the smaller size be favored?

In this study I have investigated intraspecific variation in feeding strategies in natural populations by comparing the prey selection used by the rough skinned newt, *Taricha granulosa.* This species is considered, as are other newts, to be a generalist type of carnivore feeding on virtually all soft prey with which it comes in contact and which will fit into its mouth (Pimentel, 1952; Porter, 1973; Beatty *et al,* 1976). The adult newt has an annual terrestrial phase and an aquatic phase with the latter being spent in either permanent ponds, temporary ponds, or slow-moving streams. These animals return to the same pond (or stream) each year (Twitty, 1966), which would suggest that these organisms should exhibit a feeding behavior or strategy which exemplifies the selective pressures associated with the prey availability of their respective ponds.

Permanent ponds are usually characterized as being relatively stable, having a high species diversity, and having low faunal density levels. In contrast, the temporary ponds should be less stable, exhibit less species diversity, and have high faunal density levels. This latter aspect reflects the high biotic potential often associated with temporary ponds (Welch, 1952).

In this study I have asked the following questions. Do populations of *T. granulosa* exhibit interpopulational differences in feeding strategies—eutropy versus stenotropy? If different strategies can be shown, do they reflect the nature of the pond—the presence or absence of high prey diversity?If there are differing strategies, are there any corresponding morphological differences, *e.g.,* snout-vent length (SVL) or head width, exhibited by these animals?

#### Methods and Materials

*Ponds:* Two ponds were sampled near Corvallis, Oregon during February 1975. The permanent pond was part of a series of abandoned fish ponds over 20 years old located approximately 13 km north of Corvallis. The temporary pond, which was dry during the summer months, was a quarry seep located approximately 25 km southwest of Corvallis. The permanent pond was approximately 15x50 m with a depth of 1.5 m whereas the temporary pond was 15 m in diameter with a depth of 0.5 m.

*Samples:* Fifty adults were taken from each pond and immediately fixed in FAA to preserve the stomach contents.

*Data:* For each specimen sex was determined, and SVL and head width were measured. The stomachs were removed and their contents identified down to the major groups; *i.e.,* sub-class for crustaceans, order for insects, and class for the other phyla. The numbers of each prey type were recorded.

*Statistical Analysis:* The Shannon-Wiener index from information theory was used to calculate diversity (H′) where $H' = -\sum_{1}^{s} p_i \ln p_i$. S is the number taxa or species types and $p_i$ is the proportion of the total number of individuals belonging to the ith species. Pielou's J′ was used to standardize the diversity values where $J' = H'/H_{max}$ and

$H_{max} = 1n\ S$. Comparisons were made between samples with respect to the means of their SVL and head widths. Correlation coefficients for SVL and head widths within each sample were computed.

### Results

Data from the stomach contents are presented in Table 1. Two significant points are that initially a greater number of both prey types and prey numbers were found in the temporary pond's sample; secondly, the greatest differences between the samples appear to be the number of Ostracoda and amphibian eggs. However, these data do not reflect the relative diversity values for the samples.

Table 2 presents both the results of the diversity analyses and the statistical comparisons between samples. The permanent pond sample clearly has a more diverse prey fauna, as indicated by its evenness value $J' = 0.597$, than the temporary pond sample with $J' = 0.371$. A highly significant ($p<0.01$) positive correlation was found between SVL's and head widths. Significant differences were also found between the SVL's of the different pond samples ($p<0.05$) and between the head widths ($p<0.01$).

TABLE 1. Stomach contents of newts taken from a permanent pond and a temporary pond. Number of newts sampled from each pond = 50.

| Prey* | Permanent | | Temporary | |
|---|---|---|---|---|
| | No. prey items | % of all prey | No. prey items | % of all prey |
| Ostracoda | 160 | 59.5 | 1821 | 69.1 |
| Diptera (L) | 25 | 9.3 | 5 | 0.2 |
| Amphibian eggs | 15 | 5.6 | 479 | 18.2 |
| Nematoda | 12 | 4.5 | 12 | 0.5 |
| Gastropoda | 12 | 4.5 | 67 | 2.5 |
| Oligochaeta | 7 | 2.6 | 3 | 0.1 |
| Ephemoptera (L) | 6 | 2.2 | — | — |
| Arachnida | 4 | 1.5 | — | — |
| Coleoptera (L) | 4 | 1.5 | 3 | 0.1 |
| Diptera | 4 | 1.5 | 3 | 0.1 |
| Trichoptera (L) | 3 | 1.1 | 81 | 3.1 |
| Hymenoptera | 3 | 1.1 | 1 | 0.0 |
| Collembola | — | — | 61 | 2.3 |
| Copepoda | — | — | 53 | 2.0 |
| Branchiopoda | — | — | 22 | 0.8 |
| Hirudinea | — | — | 8 | 0.3 |
| Isopoda | 1 | 0.4 | 1 | 0.0 |
| Coleoptera | 1 | 0.4 | 7 | 0.3 |
| Odonata | — | — | 2 | 0.1 |
| Lepidoptera (L) | — | — | 1 | 0.0 |
| Unidentified | 12 | 4.5 | 6 | 0.2 |
| Total | 269 | | 2636 | |
| No. of prey types (S) | 15 | | 19 | |
| No. of empty stomachs | 5 | | 0 | |

* (L) denotes larvae

TABLE 2. Diversity measurements and selected morphological measurements for newts taken from a permanent pond and a temporary pond. See text for discussion of diversity values. Data are expressed in millimeters as mean ± standard deviation. Number of animals sampled from each pond = 50.

| Statistic | Permanent | Temporary | t |
|---|---|---|---|
| Diversity | | | |
| H′ | 1.616 | 1.093 | |
| H-max | 2.708 | 2.944 | |
| J′ | 0.597 | 0.371 | |
| Morphology | | | |
| SVL | 68.67±3.71 | 70.69±4.37 | 2.49* |
| Head width | 15.80±0.91 | 16.60±1.29 | 3.58** |
| r | .582** | .683** | |

* $p<0.05$
** $p<0.01$

## Discussion

The results reveal that the two populations of *T. granulosa* have utilized different diversities of prey. However, they do not allow me to state that the temporary pond dwellers were in fact specializing since their prey selection may only reflect the diversity of prey available—and this parameter was not measured. A generalist will select items in proportion to their encounter rate, but the specialist will pick and choose with each new encounter. I would speculate that the newts do in fact eat virtually any potential prey item with which they come in contact. However, they may be specialized in their ability to locate areas of high prey density. Neish (1970) has shown that *T. granulosa* is very efficient in using scent to locate high concentrations of prey. This factor could account for the large numbers of ostracods and amphibian eggs found in the temporary pond sample.

One very significant aspect of the results is the differences in body size and head widths found between the two samples. The increased body sizes and correlated head widths found in the temporary ponds may be a reflection of the large concentrations of prey available in these ponds. Schoener (1969) has suggested that with an abundant amount of prey available to a predator, selection should favor a larger sized predator. The results I have presented may very well give credence to this hypothesis. The next logical step would obviously be to initiate a systematic comparison of newt populations inhabiting permanent and temporary ponds. One would then have to determine if there existed any correlations between pond type and body size. In order to conduct this study properly, the direct comparisons between pond types must be restricted geographically since there may be either clinal or geographical phenotypic variations in the body sizes which are independent of pond types and which would subsequently bias any observations.

In summary I have shown that there was a difference in the diversity of utilized prey between samples taken from a permanent pond and those taken from a temporary pond. I have not demonstrated that there was a true difference in feeding strategies. Finally, I believe that the differences in body size may be a reflection of the relative abundance of prey in the respective ponds.

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# Trends in Plant Species Diversity Associated with Development in a Series of Pseudotsuga menziesii/Gaultheria shallon Stands

## Abstract

Plant species diversity of a chronosequence of *Pseudotsuga menziesii/Gaultheria shallon* stands is related to changes in stand structure. It is hypothesized that trends in diversity of many plant communities may reflect rapid changes in the status of dominant species during the early stages of community development. This hypothesis is initially tested by examining trends in species diversity of several developing plant communities as reported in the literature.

## Introduction

Species diversity has been defined as the relationship between number of species present in a population or sample and relative importance of those species (Odum, 1971). As a population statistic, diversity has been related to stability (Odum, 1969), succession (Margalef, 1968), environmental stress (Grimes, 1973; del Moral, 1972), predator pressure (Janzen, 1969; Paine, 1966), spatial patterns (Pielou, 1966) and ecosystem productivity (Connell and Orias, 1964).

To understand the functioning of an ecosystem, however, one must have more than a correlation between diversity and some other ecosystem parameter (Hurlbert, 1971). Cause-and-effect relationships between diversity and other ecosystem parameters can only be understood from identification and study of mechanisms responsible. This process implies a need to know the role of individual species in controlling community diversity.

The literature abounds with examples of the strengths and weaknesses of diversity as an index of functional relationships between organisms in a population. The often cited connection between stability and diversity, in the form of food web complexity, has been shown in at least one ecosystem to depend on the nature of relationships between specific organisms (Paine, 1966). The possibility of predicting competitive relationships by use of species diversity relates directly to studies of communities of higher plants. For example, diversity has been used in calculating estimates of niche width and overlap (Levins, 1968; Pielou, 1972).

Much speculation but little study has been devoted to associations between changes in plant species diversity and community development (Loucks, 1970). Until recently the consensus seemed to be that diversity increases with time following disturbance, either asymptotically to a relatively high equilibrium or perhaps to a peak, followed by a slight decrease in diversity (Odum, 1969; AuClair and Goff, 1971). However, this commonly accepted pattern is by no means universal (Perino and Risser, 1972; Shafi and Yarranton, 1973; Bazzaz, 1975).

The purposes of this paper are: (1) to discuss the pattern of change in plant species diversity with time for a forest community dominated by *Pseudotsuga menziesii* (Mirb.) Franco and *Gaultheria shallon* Pursh; (2) to suggest mechanisms responsible for this

pattern; and (3) to propose a general hypothesis for explaining patterns of species diversity in early stages of community development.

### Site Description

The study was conducted on the A. E. Thomson Research Center in the City of Seattle's Cedar River watershed. The area is located 30 km east of Seattle at approximately 47° 50°N and 122°W in the foothills of the Cascade Mountains. Elevation at the study area is approximately 220 m. Mean annual precipitation is 144 cm, most of which falls in the winter as rain. The mean temperatures in July and January are 17 and 3 C.

Study plots were established in five stands of different ages (5, 22, 30, 45 and 73 years). The four older stands were naturally regenerated following fires which occurred after the area was logged in the first quarter of this century (Long and Turner, 1975). The five-year-old stand originated following the recent clearcutting of a stand not cut during the earlier period of logging activity. Each of the stands is on level ground on soil of the Everett Series (Topic Haplorthod). This well-drained soil, derived from glacial till, is gravelly with only 5 percent clay and silt (Turner and Long, 1975). The stands are typical of the *Pseudotsuga menziesii/Gaultheria shallon* community described by Becking (1954). Mensurational details for the four older stands are presented in Table 1; each of the stands have a relatively low site quality (site index IV). Patterns of biomass accumulation and production for this series of stands have been previously reported (Long and Turner, 1975; Turner and Long, 1975).

### Methods

Five randomly located plots were established in each of the stands. The plots were 15- x 25-m except for those established in the 22-year-old stand; 5- x 25-m plots were used in this relatively dense and uniform stand. The plots were laid out using hand compass and tapes. Canopy cover for each understory species was estimated on two hundred fifty 20- x 50-cm subplots within each stand. Fifty of these subplots were located at 1 m intervals along two lines, 5 m apart, running parallel to the long axis of each of the larger plots (Daubenmire, 1959).

Data collected on each of the large plots included the diameter at breast height (dbh), 1.4 m from the base, of all trees greater than 2.54 cm dbh. A spherical mirror with an etched grid was used to estimate total overstory cover (Lemmon, 1956). The estimate for each stand represents an average of 36 readings taken at 5 m intervals along four arbitrarily located lines within the stand. Determinations of soil type were made from a pit in the center of each plot.

An estimate of cover for each understory species occurring in the subplots was based on six cover classes: (1) 0-5 percent; (2) 6-25 percent; (3) 26-50 percent; (4) 51-75 percent; (5) 76-95 percent; (6) 96-100 percent. The mid-points of the various cover classes were used in deriving an estimate of average cover for each species in a stand (Daubenmire, 1959).

Diversity indices, of which there are many, estimate different aspects of the allocation of importance between species (Hill, 1973). The diversity of a particular sample has two components—the relative abundance of different species in the sample and the degree to which their relative importance is apportioned among the species. This second component of diversity is referred to as evenness (Pielou, 1969).

TABLE 1. Density (stems per hectare), basal area (square meters per hectare), and average dbh (centimeters) of the species of the overstory for the stands in the study (excluding the five-year-old stand).

| | Stand age (yr) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 22 | 30 | 42 | 73 | 22 | 30 | 42 | 73 | 22 | 30 | 42 | 73 |
| | Density (stems/ha) | | | | Basal area ($m^2$/ha) | | | | Average diameter (cm) | | | |
| *Alnus rubra* Bong. | 16 | | | | 0.07 | | | | 7.4 | | | |
| *Cornus nuttalli* Aud ex T. & G. | | 5 | | | | 0.01 | | | | 5.0 | | |
| *Pseudotsuga menziesii* (Mirbel) Franco. | 1616 | 1872 | 527 | 651 | 17.98 | 21.35 | 25.53 | 30.62 | 11.9 | 12.0 | 24.7 | 24.5 |
| *Rhamnus purshiana* DC | | 5 | | | | 0.23 | | | | 24.0 | | |
| *Thuja plicata* Donn | | | | 43 | | | | 0.38 | | | | |
| *Tsuga heterophylla* (Raf. Sarq. | 32 | 59 | 13 | 443 | 0.06 | 0.51 | 0.07 | 13.82 | 4.9 | 10.4 | 8.2 | 19.9 |
| TOTAL | 1664 | 1941 | 540 | 1137 | 18.02 | 22.10 | 25.60 | 44.82 | | | | |

Species diversity was computed for each stand using Brillouin's (1962) index—$H = (1/N!\ (\log_2(N!/n_1!n_2!\ ....n_i!)$, where: H is diversity in bits per plant unit; N is the total number of plant units in the sample, and $n_i$ is the number of plant units for the $i^{th}$ species. The evenness component of diversity was calculated using Pielou's (1969) index—$J = H/\log_2 S$, where: H is Brillouin's index and S is the number of species.

The use of factorials in the calculation of the diversity index necessitates the transformation of the data from percent cover to integers. The units used were $cm^2$. This transformation is a computational necessity and should not be viewed as an attempt to increase the precision of the original data. Since the data did not include estimates of canopy cover for individual tree species, a percentage of the total canopy cover for individual tree species, a percentage of the total canopy cover was apportioned to each tree species present in a sample based on the species' contribution to total stem cross-sectional area at breast height (Reiners *et al.*, 1971).

#### Results and Discussion

The estimates of cover for understory species present on the study plots are presented in Table 2. The estimates of total overstory canopy cover in each stand are: 5-year-old stand—0 percent; 22-year-old stand—71 percent; 30-year-old stand—74 percent; 42-year-old stand—82 percent; 73-year-old stand—86 percent.

The pattern of species diversity with respect to time observed for the *Pseudotsuga menziesii/Gaultheria shallon* stands studied does not conform to the suggested trend (*i.e.,* a monotonic increase) for early to middle successional stages (Fig. 1). Rather the pattern is one of a decrease in species diversity from the 5-year-old stand to the 22-year-old stand and a general increase in diversity thereafter, up to the limit of the study (73 years). The evenness component of diversity decreases from a maximum in the 5-year-old stand to a minimum in the 22-year-old stand and increases in each of the remaining age classes (Table 3).

While the 5-year-old stand has the lowest total cover (Table 2) of the stands examined in this study, it has the highest species richness and diversity. In a similar vegetation type, Dyrness (1973) found this age class to represent a period in succession with the most rapid addition of opportunistic species. In contrast to the 5-year-old stand, the understory of the 22-year-old stand is dominated by *G. shallon.* The developing overstory of this stand apparently provides the degree of canopy under which *G. shallon,* with a reduction in light intensity and evaporative demand, achieves its best development (Swank, 1972). The 65 percent cover of this shrub species represents 59 percent of the total understory cover.

The abundance of *G. shallon* in the 22-year-old stand is associated with relatively depauperate herb and moss layers. This lack of diversity is presumed to be in large part the result of the environment created beneath the heavy *G. shallon* subcanopy. Not only are all opportunistic species, with the exception of a single moss species, excluded from this stand, but many forest understory species common to the other stands are absent as well. Figure 2 shows a strong negative relationship between herb and moss layer diversity and the coverage of *G. shallon* in these different-aged stands.

With the further development of overstory foliar biomass, *G. shallon* is adversely affected. Structural analysis of these stands (Long and Turner, 1975) demonstrates the inverse relationship between *G. shallon* and the weight of overstory foliage. To the

TABLE 2. Percent groundcover of understory species (+ indicates presence in trace amounts).

| Species | Stand age (yr) | | | | |
|---|---|---|---|---|---|
| | 5 | 22 | 30 | 42 | 73 |
| *SMALL TREE & TALL SHRUB LAYER* | | | | | |
| *Acer circinatum* Pursh | 0.01 | | 0.76 | 5.50 | 12.70 |
| *Alnus rubra* Bong. | 3.02 | 1.02 | | | |
| *Cornus nuttallii* Aud. ex T. & G. | | | 0.75 | | |
| *Holodiscus discolor* (Pursh) Maxim. | 1.72 | 4.46 | 3.34 | 2.13 | 2.84 |
| *Pseudotsuga menziesii* (Mirbel) Franco | 2.52 | 7.53 | 8.32 | 3.00 | |
| *Rhamnus purshiana* DC. | | | | 0.33 | 0.28 |
| *Salix* sp. | 0.90 | | | | |
| *Taxus brevifolia* Nutt. | | | 0.40 | | |
| *Thuja plicata* Donn | 0.03 | | | | |
| *Tsuga heterophylla* (Raf.) Sarg. | 8.36 | 6.45 | 0.52 | 0.67 | 5.00 |
| *Vaccinium parvifolium* Smith | 0.01 | 0.80 | 3.76 | 1.80 | 1.32 |
| *LOW SHRUB LAYER* | | | | | |
| *Berberis nervosa* Pursh | 4.06 | 1.94 | 1.44 | 1.96 | 1.92 |
| *Gaultheria shallon* Pursh | 12.22 | 65.26 | 44.56 | 43.72 | 30.90 |
| *Rosa gymnocarpa* Nutt. | + | 0.84 | 0.66 | + | + |
| *Rubus laciniatus* Willd. | 0.42 | | | | |
| *Rubus ursinus* Cham. & Schlecht. | 11.24 | 2.88 | 3.46 | 2.70 | 0.80 |
| *Symphoricarpos albus* (L.) Blake | | 0.20 | | | |
| *HERB LAYER* | | | | | |
| *Agrostis tenuis* Sibth. | 0.66 | | | | |
| *Anaphalis margaritacea* (L.) B. & H. | 7.24 | + | 0.02 | | |
| *Aquilegia formosa* Fisch. | | | 0.01 | | |
| *Athyrium filix-femina* (L.) Roth | 0.16 | | | | |
| *Blechnum spicant* (L.) With. | 0.18 | | | | + |
| *Campanula scouleri* Hook. ex A.DC. | | 0.02 | 0.14 | 0.02 | |
| *Carex* spp. | 0.22 | | | | |
| *Chimaphila menziesii* (R. Br.) Spreng. | | | + | | |
| *Cirsium* sp. | 0.70 | | | | |
| *Cryptogramma crispa* (L.) R. Br. ex Hook. | + | | | | |
| *Digitalis purpurea* L. | 0.36 | | | | |
| *Epilobium angustifolium* L. | 1.14 | | | | |
| *Epilobium minutum* Lindl. ex Hook. | 1.02 | | | | |
| *Galium triflorum* Michx. | 1.30 | | | | |
| *Gnaphalium uliginosum* L. | 0.01 | | | | |
| Unidentified grasses | 0.26 | | | | |
| *Hypochaeris radicata* L. | 17.76 | | | | |
| *Hypopitys monotropa* Crantz | | | | | + |
| *Linnaea borealis* L. | 2.60 | + | 3.18 | 4.26 | 23.14 |
| *Lonicera ciliosa* (Pursh) DC. | | | 0.68 | | + |
| *Lotus micranthus* Benth. | 1.36 | | | | |
| *Luzula parviflora* (Ehrh.) Desv. | 0.64 | | | | |
| *Petasites frigidus* (L.) Fried | 0.08 | | | | |
| *Polystichum munitum* (Kaulf.) Presi | 1.32 | + | 0.20 | 1.56 | 1.30 |
| *Pteridium aquilinum* (L.) Kuhn | 25.28 | 16.46 | 28.50 | 21.88 | 4.14 |
| *Spiraea douglasii* Hook. | 0.84 | | | | |
| *Streptopus amplexifolius* (L.) DC. | | | | | 0.16 |
| *Trientalis latifolia* Hook. | 0.74 | 0.26 | 0.60 | 0.80 | 0.04 |
| *Trillium ovatum* Pursh | | | 0.80 | + | 0.28 |
| *Viola sempervirens* Greene | 1.20 | 0.04 | 0.01 | 0.92 | + |
| *MOSS LAYER* | | | | | |
| *Dicranella heteromalla* (Hedw.) Schimp. | 1.58 | 0.02 | | | |
| *Dicranum fuscescens* Turn. | 0.04 | | 0.02 | 00.4 | 0.12 |
| *Eurhynchium oreganum* (Sull.) Jaeg. & Sauerb. | 0.16 | 3.46 | 25.44 | 33.92 | 5.12 |
| *Hylocomium splendens* (Hedw.) B.S.G. | | | 0.96 | 0.02 | 36.16 |
| *Minum insigne* Mitt. | | 0.06 | 0.01 | 0.08 | 0.12 |
| *Minum spinulosum* B.S.G. | | | | | 0.78 |
| *Polytrichum juniperinum* Hedw. | 0.12 | | + | 0.01 | |
| *Rhytidiadelphus loreus* (Hedw.) Warnst. | + | 0.02 | 0.64 | 0.16 | 4.74 |
| *Rhytidiadelphus triquetrus* (Hedw.) Warnst. | | | 0.06 | + | 1.44 |
| TOTALS | 11.48 | 111.02 | 128.60 | 125.48 | 133.02 |

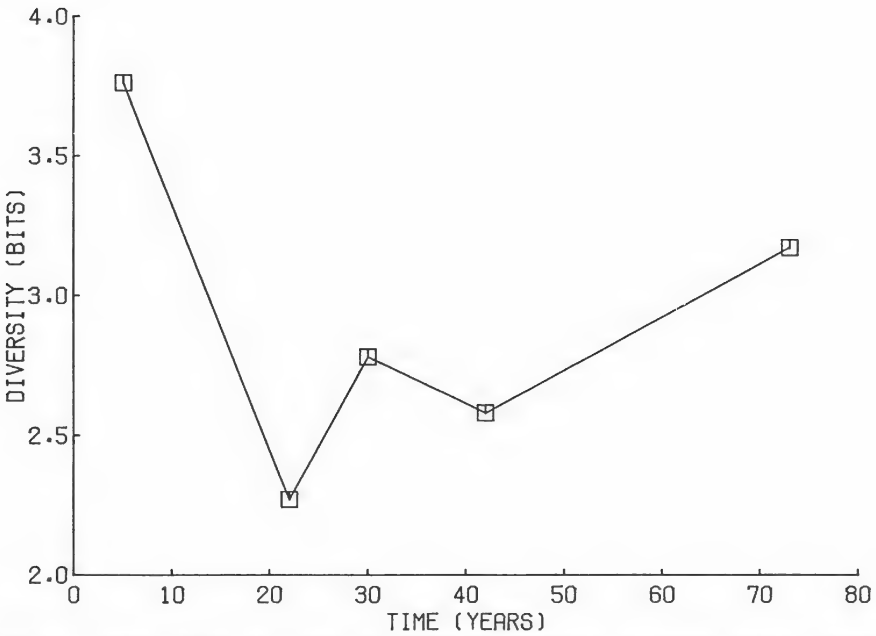


Figure 1. Species diversity for a series of different-aged *Pseudotsuga menziesii/Gaultheria shallon* stands.

extent that this relationship implies causation, it appears that the amount of foliage in the overstory determines the importance, in terms of cover and aboveground biomass, of *G. shallon* in the understory. As the relative importance of *G. shallon* declines in the older stands of this chronosequence, diversity increases.

The 73-year-old stand probably represents a relatively stable period in the development of this plant community (Long and Turner, 1975). Diversity for this stand is the highest of any stand studied with the exception of the 5-year-old clearcut. The rate of change in canopy development and species cover and composition have decreased by this stage of stand development. The decrease in *G. shallon* is associated with the increase in importance of those species tolerant of the environment created by the overstory, or perhaps intolerant of a dense subcanopy of *G. shallon.*

It may be further postulated that, if the impact of the overstory of the 73-year-old stand has stabilized, as has been suggested (Long and Turner, 1975), the understory may also be approaching a similar dynamic equilibrium in terms of species richness, diversity, and cover. There will be continued growth of such large, long-lived shrubs as

TABLE 3. Richness (number of species), evenness (Pielou, 1966), and diversity (Brillouin, 1962) for five different-aged *Pseudotsuga menziessi/Gaultheria shallon* stands.

| | Stand age (yr) | | | | |
|---|---|---|---|---|---|
| | 5 | 22 | 30 | 42 | 73 |
| Richness | 41 | 19 | 31 | 24 | 23 |
| Evenness | 0.70 | 0.51 | 0.55 | 0.55 | 0.66 |
| Diversity | 3.76 | 2.27 | 2.78 | 2.58 | 3.17 |

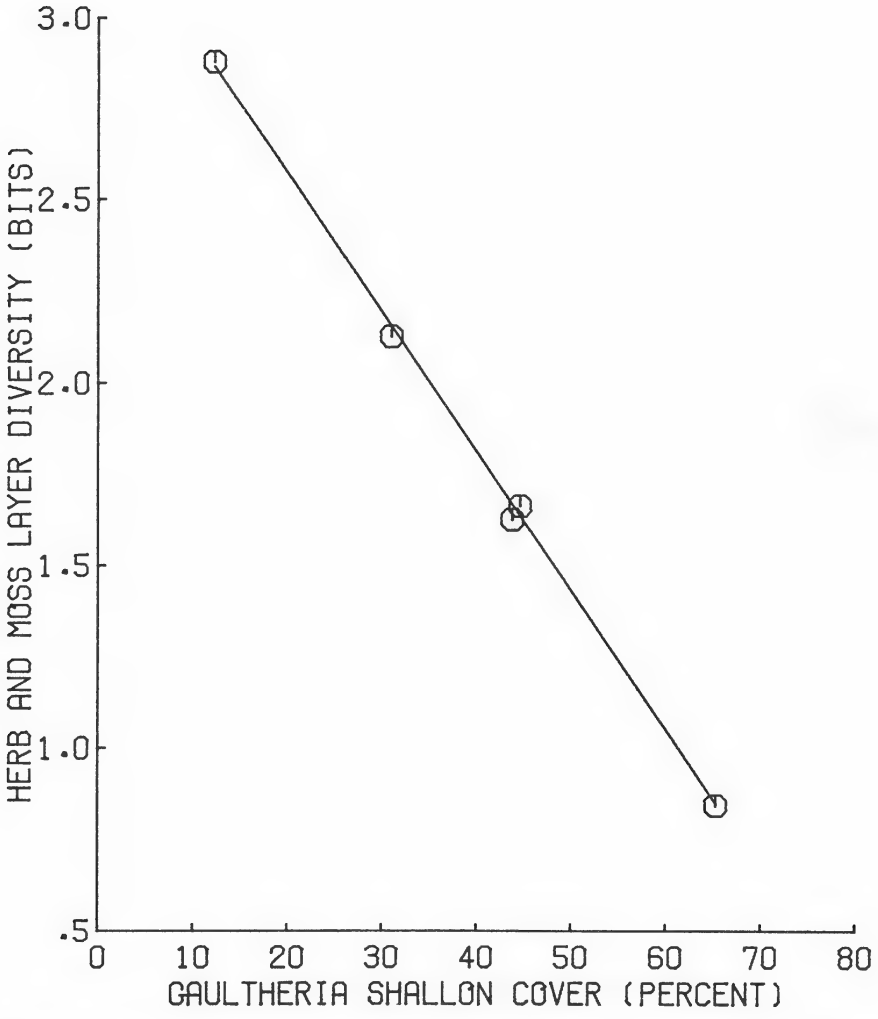


Figure 2. The relationship between herb and moss layer diversity and *Gaultheria shallon* cover. $Y = 3.333 - 0.038X$; $R^2 = 0.99$.

*Acer circinatum* Pursh. Nevertheless, the rate of change in the understory has almost certainly slowed drastically relative to the preceding stages of stand development. Circumstantial evidence for this contention is provided by the comparison of diversity values from this study with those calculated from data of Dyrness (1973). The ratio of species diversity in the 73-year-old stand to diversity in the 5-year-old stand is 84 percent. This ratio is similar to the 85 percent obtained by comparing diversity in Dyrness' 300- to 500-year-old *P. menziesii* stands before, and five years following logging and fire.

Climax, as the term is normally applied, will not occur in these stands for at least several hundred years. Changes occurring during this period will include an increasingly

more important role, in terms of cover and density, for *Tsuga heterophylla* (Raf.) Sarg. as a component of both understory and overstory. Barring disturbance, *P. menziesii* will gradually be replaced by *T. heterophylla* as the predominant species in the overstory. The effects on the understory of an overstory canopy composed predominantly of a late successional species such as *T. heterophylla,* as opposed to a pioneer such as *P. menziesii,* will undoubtedly result in changes within the subordinate vegetation (Horn, 1971). The nature and extent of these changes cannot be predicted on the basis of this investigation; however, it can be logically assumed that, because the future changes in the overstory will be gradual, further changes in the composition and structure of the understory will also be slow relative to the dynamic period of stand development represented in this study.

On the basis of the observed pattern in species diversity and the suggested relationships between diversity and stand structure for the *Pseudotsuga/Gaultheria* community, the following hypothesis is suggested. As succession proceeds in a terrestrial plant community, particularly in the early stages when changes in the relative ecological status of individual species are often quite rapid, changes in the direction in which diversity is proceeding are to be expected. It is suggested that species diversity is a function of the individual species present in a community and thus as an ecological index means little outside the context of those interactions.

In an initial test of the plausibility of the hypothesis, diversity patterns for several chronosequences from literature were compared. The criteria for selection were: (1) the availability of sufficient data for the calculation of diversity and the identification of species relationships, and (2) the inclusion of sufficient successional stages from which to infer a pattern. A chronosequence chosen on this basis was one representing primary succession at Glacier Bay, Alaska (Reiners *et al.,* 1971). One of the characteristics of the trend in diversity with successional development is the decrease in diversity at about 33 years following deglaciation. This dip in diversity corresponds to a rather large increase in the relative importance of *Dryas drummondii* Richards during this stage of succession. As community development and overstory canopy closure proceed, and the importance of *D. drummondii* is reduced, diversity increases. Reiners *et al.* (1971) speculate that other, unsampled stages in this chronosequence might have similar decreases in diversity also attributable to temporary dominance by particular species.

The patterns of change in diversity discussed so far are for the relationships between rather broad successional stages. During the first several years following initiation of secondary succession, however, the year-to-year replacement of species and, more specifically, the rapid change in the relative status of species within the community may result in considerable modification of diversity (Bazzaz, 1975). The data presented by Dyrness (1973) for the first five years following the logging and burning of an old-growth *Pseudotusga menziesii* stand were used to calculate diversity for this rapidly changing community (Fig. 3). In the first year following burning, diversity increased to a relatively high level; however, by the second year diversity was reduced. This decrease was followed by a gradual increase over the next three years. The decrease in diversity in the second year was associated with the rapid achievement of dominance by *Senecio sylvaticus L.* and *Epilobium* spp. While these opportunistic species accounted for only 27 percent of total community cover during the first year following burning, they con-

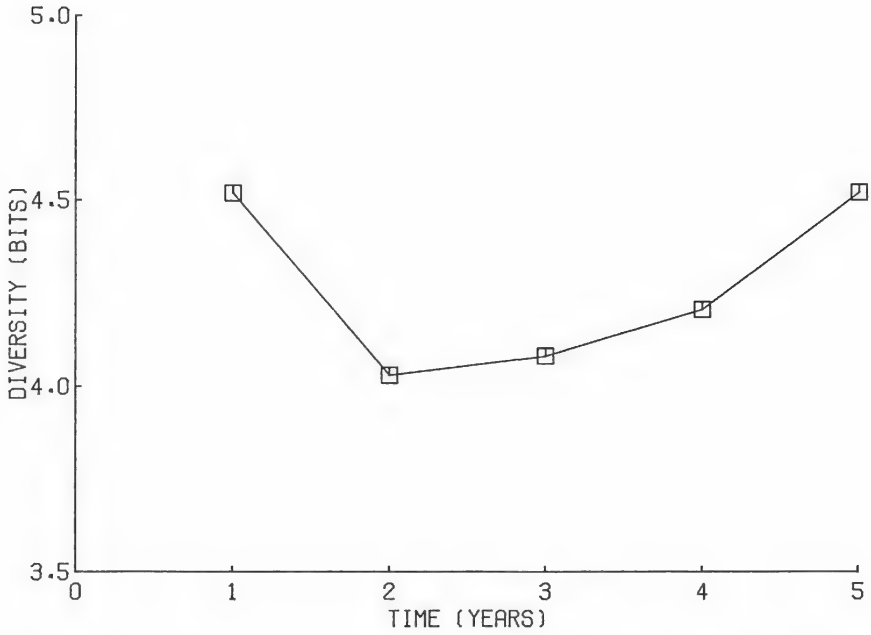


Figure 3. Changes in species diversity with time following logging and burning of an old-growth *Pseudotsuga menziesii* forest (Dyrness, 1973).

tributed 59 percent of total cover by the third year. Their contribution decreased gradually in each of the remaining years.

Not all of the successional sequences examined exhibit the same trend in diversity. Henderson's (1970) study of different-aged *Alnus rubra* Bong. stands provides data from which diversity for the first 50-60 years of secondary succession can be calculated (Fig. 4). Henderson discounts the representativeness of the oldest stand in the series as a result of grazing and flooding. If this stand is excluded, the pattern of diversity appears to be one of an initial rapid increase followed by a gradual decline. It is suggested that basic differences in stand structure account for the different patterns in species diversity observed for the *Alnus* and *Pseudotsuga* communities. Unlike most forest stands, an Alnus-dominated community may achieve canopy closure within the first several years of stand development. Henderson's data in fact indicate 99 percent canopy closure for the two-year-old stand, which represents the first point in his chronosequence. Canopy closure decreases linearly with age for the remainder of the chronosequence. This aspect of changing stand structure may at least partially explain the observed general increase in species diversity for the first 25 years of stand succession.

Henderson (1970) points out that as the *Alnus* overstory is reduced by natural thinning, *Rubus spectabilis* Pursh. increases in dominance and may eventually form the major component of a shrub-dominated stage of succession. The increase in cover and biomass of *R. spectabilis* with time, beginning with the 25-year-old stand, coincides with the slight downward trend in species diversity. It is suggested that *R. spectabilis* may have a similar relationship in diversity within the *Alnus* community as does *Gaultheria*

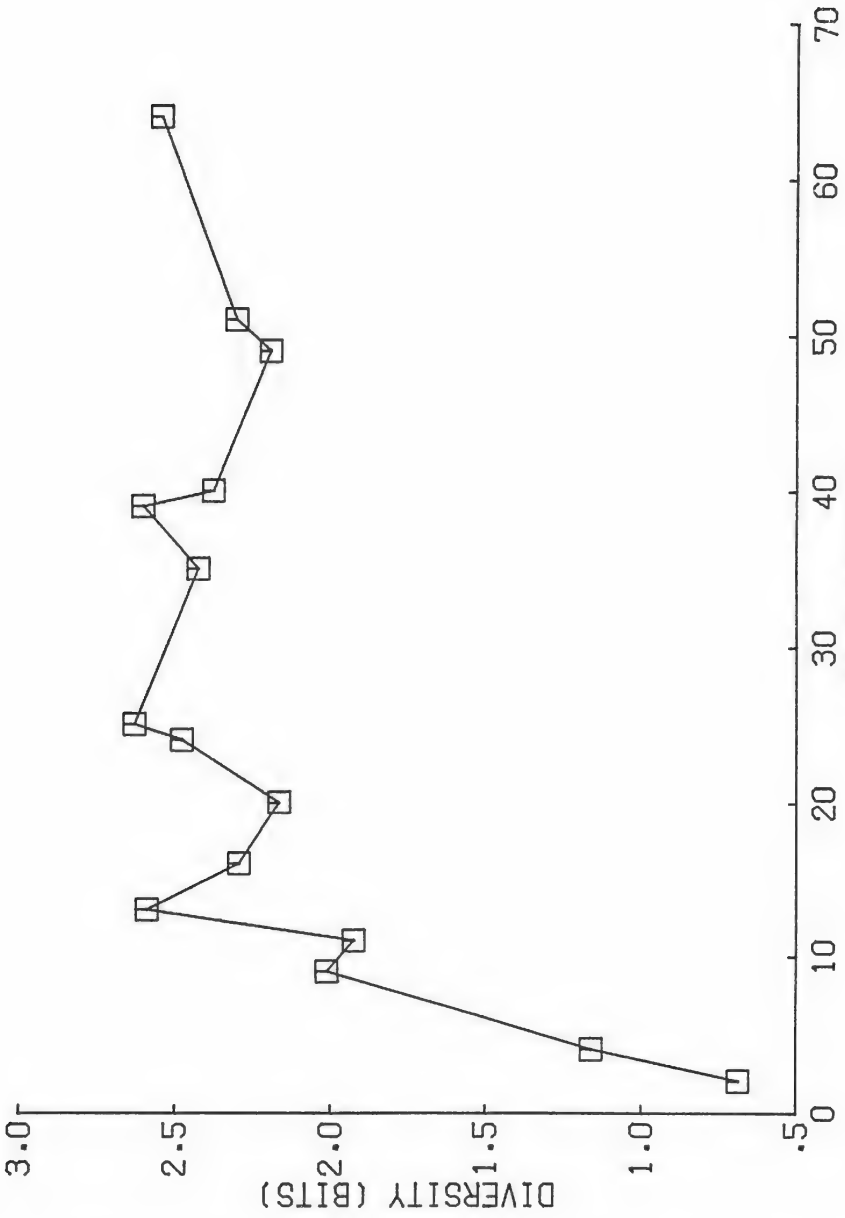


Figure 4. Species diversity for a series of different-aged *Alnus rubra* stands (Henderson, 1970).

*shallon* within the *Pseudotsuga menziesii* community. The main difference is that while *G. shallon* achieves its peak in dominance prior to stand canopy closure, *R. spectabilis* does not begin to achieve dominance until the decline of the original stand canopy.

## Summary and Conclusions

The relationships between species diversity and various aspects of stand structure for a *Pseudotsuga menziesii/Gaultheria shallon* chronosequence were investigated. A pattern of change in diversity with advancing succession is described wherein the initial high diversity of the community type following the initiation of secondary succession is reduced by the nearly complete, but temporary, domination of the understory by a shrub, *G. shallon.* Subsequently, as the relative importance of *G. shallon* is reduced by overstory canopy closure, diversity begins to increase. It is suggested that the pattern of diversity during the initial stages of stand development in this community is most usefully analyzed in the context of changes in community structure.

Limitations imposed on this analysis of changing diversity by possible deficiencies in the sample size and the chronosequence approach are not considered to be serious. It is not the details of the pattern that are important, but rather the postulation that changing plant community diversity is a function of community structure.

Based on these observations it is hypothesized that trends in diversity of many communities may reflect the rapid changes in the relative status of individual species during the dynamic early stages of community development. The analysis of changing community structure may help to resolve some of the ambiguity associated with diversity and its relationship to succession.

## Acknowledgment

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**CORRECTION**

On page 211 of the November, 1976 issue (paper by E. R. Falkenhagen) there were errors in the printing of the Duncan's test; these three lines should have appeared as follows:

The Duncan's test for potassium is as follows ($\alpha = 0.05$):

| Provenance | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| number | 3 | 32 | 40 | 15 | 25 | 4 | 37 | 27 | 28 | 23 |

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# Enhancement of Methylmercury Uptake in Fish by Lake Temperature, pH, and Dissolved Oxygen Gradients: Hypothesis

## Abstract

Mercury analyses of fish tissue from two Oregon, U.S.A., lakes showed higher mercury concentrations in fish from a "eutrophic" lake than in fish from an adjacent "oligotrophic" type. This finding was attributed to differences between lakes regarding certain physical-chemical vertical gradients. In summer, the eutrophic lake developed thermal, pH, and dissolved oxygen conditions which may have contributed to higher rates of methylmercury uptake in fish. Conversely, fish in the oligotrophic lake were not subjected to these conditions, and consequently accumulated less mercury.

## Introduction

Mercury levels in fish are reportedly higher for oligotrophic lakes than eutrophic ones, provided both lake types are similarly contaminated with mercury (Jernelöv *et al.* 1975). This fact is caused by (1) the large biomass unit$^{-1}$ volume eutrophic lakewater which makes less mercury available unit$^{-1}$ biomass, (2) the supposed higher efficiency of energy transfer between trophic levels in oligotrophic lakes which concentrates more mercury in the higher carnivores and (3) the generally lower pH of oligotrophic lakes which tends to form biologically-available monomethyl mercury rather than the volatile dimethyl type.

Lake studies in Oregon, U.S.A., indicate that other factors promote mercury uptake in fish. These factors may have caused the high mercury concentrations in fish from a "eutrophic" lake which exceeded levels found in fish from an adjacent "oligotrophic" type.

## Lake Descriptions

The study lakes, Big Squaw and Upper Squaw lakes, are located in southwestern Oregon, approximately 4 km north of the Oregon-California border, and 105 km east of the Pacific Coast. The lakes lie within a few hundred meters of one another in the vicinity of at least one former mercury mining site. Cinnabar deposits, associated with serpentine and diorite rocks, are found in the general area.

Upper Squaw Lake lies at elevation 777 m, has a surface area of 0.082 km$^2$, reaches a maximum depth of 16 m and drains into Big Squaw Lake via Squaw Creek. Big Squaw Lake, elevation 762 m, has a surface area of 0.196 km$^2$, reaches its maximum depth at 34 m and is impounded by a small earth-filled dam at its west end.

Big Squaw Lake is less productive biologically than the upper lake, caused, in part, by its deep, steep-sided morphometry. Upper Squaw Lake is truly eutrophic, featuring substantial blooms of bluegreen algae *(Anabaena sp.)* which did not appear in Big Squaw during the study.

Mercury concentrations in Big Squaw Lake sediment samples differed substantially from Upper Squaw sediments. Average total mercury concentration per three sediment samples from the upper lake (0.51, 0.61, 0.56 $\mu g\ g^{-1}$) was 0.56 $\mu g\ g^{-1}$, or double the amount for Big Squaw (0.20, 0.30, 0.26 $\mu g\ g^{-1}$; $\bar{x} = 0.25\ \mu g\ g^{-1}$), (unpublished data courtesy Umpqua Research Company, Myrtle Creek, Oregon).

#### Procedures

Several fish species were collected from Squaw Lakes on 23, 24 April and 21, 22 August, 1975. Collections were made using graduated mesh gill nets (stretch mesh 1.3-5.1 cm) set at right angles to the shoreline for overnight periods of about 14 hours. Nets were retrieved the following day. Gilled fish were identified, weighed, measured (fork length), tagged, placed individually in plastic bags and stored in ice. Mercury analyses of fish tissues were initiated within four hours of collection. Whole fish were placed in a blender and reduced to a fine slurry. This slurry was subsampled for total mercury analysis by sulfuric acid digestion and flameless atomic absorption technique (Uthe *et al.,* 1970; Thorpe, 1971).

Some fish from the April study were delivered to the U.S. Food and Drug Administration (FDA) lab in Seattle, Washington, U.S.A., for mercury analyses. These were frozen, and analyzed for total mercury about six weeks later. Fish were grouped according to species, and each species was composited for analysis. Analyses were performed on "edible" parts of composites of each species (*i.e.,* only muscle tissue). Determination of total mercury was by cold vapor atomic absorption method, using sulfuric/nitric acid digestion with vanadium pentoxide catalyst.

Temperature and dissolved oxygen vertical profiles were obtained for each lake on 25 July and 22 August. Temperature was measured with a Yellowsprings Model 43TD tele-thermometer (scale calibrated in 1.0°C units). D.O. determinations were by Winkler method (azide modification). pH was measured with Corning Model 610A pH meter (expanded scale) on 25 July.

#### Results and Discussion

Average concentrations of total mercury in Upper Squaw Lake fish were double the levels detected in the same species from the lower, more "oligotrophic" lake (Table 1). Composited fish analyses by FDA produced similar results (Table 2), although FDA values were relatively higher than those obtained by the private lab. This difference was caused, perhaps, by differences between laboratory digestion techniques or analytical methods (*e.g.,* composite versus individual fish, "edible" portion versus whole fish, delayed versus immediate analyses).

Limnological studies indicated that the lakes were gradually depleted of dissolved oxygen in deep waters during summer (Table 3). By August, Upper Squaw Lake was anaerobic, or nearly so, between nine meters and the bottom. The concentration of dissolved oxygen in the 6-9 m stratum, particularly during early morning, appeared to be intolerably low for fish (Table 3). Big Squaw Lake was well-oxygenated ($>5.0$ mg/1) in the top 20 m (Table 3), but was anaerobic along the bottom.

Both lakes developed relatively high temperature and pH conditions in the 0-4 m stratum during summer. Temperatures in the upper layers exceeded 16.0°C, and pH reached 9.1 in Upper Squaw Lake during a July algal bloom (Table 3).

TABLE 1. Concentrations of total mercury (wet weight basis) in Squaw Lakes Fish.

| 23-24 April | | | | |
|---|---|---|---|---|
| Lake[a] | Species[b] | Weight (g) | Fork length (cm) | Mercury conc (p.p.m.) |
| U.S. | CT | 74.1 | 19.6 | 0.216 |
| U.S. | CT | 45.6 | 17.3 | 0.047 |
| U.S. | CT | 122.5 | 24.1 | 0.220 |
| U.S. | CT | 109.0 | 22.9 | 0.268 |
| U.S. | CT | 102.9 | 22.1 | 0.240 |
| U.S. | CT | 120.3 | 23.6 | 0.222 |
| U.S. | CT | 82.8 | 20.8 | 0.190 |
| U.S. | CT | 88.3 | 21.6 | 0.213 |
| U.S. | CT | 81.4 | 20.6 | 0.264 |
| U.S. | CT | 88.0 | 21.6 | 0.218 |
| U.S. | CT | 72.8 | 19.3 | 0.159 |
| U.S. | CT | 91.6 | 20.8 | 0.174 |
| U.S. | CT | 69.3 | 19.1 | 0.312 |
| U.S. | CT | 69.0 | 18.3 | 0.167 |
| U.S. | CT | 47.8 | 17.3 | 0.222 |
| | | | | 0.205 ($\bar{x}$) |
| B.S. | CT-RB | 175.0 | 25.9 | 0.078 |
| B.S. | CT-RB | 203.7 | 26.2 | 0.099 |
| B.S. | CT-RB | 182.8 | 25.9 | 0.100 |
| B.S. | CT-RB | 150.0 | 24.9 | 0.082 |
| | | | | 0.090 ($\bar{x}$) |
| B.S. | BH | 63.4 | 17.3 | 0.046 |
| B.S. | BH | 84.5 | 18.3 | 0.051 |
| B.S. | BH | 90.9 | 19.1 | 0.049 |
| | | | | 0.049 ($\bar{x}$) |
| B.S. | BC | 35.0 | 13.0 | 0.067 |
| B.S. | BC | 39.7 | 13.7 | 0.075 |
| B.S. | BC | 53.0 | 15.2 | 0.044 |
| B.S. | BC | 49.1 | 14.7 | 0.053 |
| B.S. | BC | 41.1 | 14.2 | 0.044 |
| B.S. | BC | 46.9 | 14.2 | 0.064 |
| B.S. | BC | 50.8 | 15.0 | 0.054 |
| B.S. | BC | 45.4 | 14.7 | 0.078 |
| B.S. | BC | 45.4 | 14.2 | 0.083 |
| B.S. | BC | 46.2 | 15.5 | 0.068 |
| B.S. | BC | 46.4 | 14.5 | 0.064 |
| B.S. | BC | 43.8 | 14.2 | 0.050 |
| B.S. | BC | 38.0 | 14.5 | 0.048 |
| B.S. | BC | 40.5 | 14.2 | 0.063 |
| B.S. | BC | 40.8 | 14.0 | 0.070 |
| B.S. | BC | 41.5 | 14.0 | 0.056 |
| B.S. | BC | 41.1 | 14.2 | 0.066 |
| B.S. | BC | 41.3 | 14.0 | 0.120 |
| B.S. | BC | 37.2 | 13.2 | 0.061 |
| B.S. | BC | 41.1 | 14.0 | 0.048 |
| B.S. | BC | 50.0 | 15.0 | 0.050 |
| B.S. | BC | 41.2 | 14.0 | 0.074 |
| B.S. | BC | 44.9 | 14.0 | 0.048 |
| B.S. | BC | 44.8 | 14.0 | 0.071 |
| B.S. | BC | 36.1 | 13.7 | 0.048 |

TABLE 1. (continued)

| | | | | |
|---|---|---|---|---|
| B.S. | BC | 49.5 | 14.5 | 0.048 |
| B.S. | BC | 51.2 | 15.2 | 0.068 |
| B.S. | BC | 37.0 | 13.7 | 0.048 |
| B.S. | BC | 43.9 | 13.7 | 0.061 |
| B.S. | BC | 33.0 | 13.5 | 0.052 |
| | | | | 0.059 ($\bar{x}$) |
| | | 21-22 August | | |
| U.S. | CT-RB | 61.8 | 18.8 | 0.018 |
| U.S. | CT-RB | 66.4 | 19.1 | 0.053 |
| U.S. | CT-RB | 61.7 | 19.4 | 0.123 |
| U.S. | CT-RB | 55.8 | 18.8 | 0.158 |
| U.S. | CT-RB | 96.6 | 22.9 | 0.193 |
| U.S. | CT-RB | 57.1 | 18.1 | 0.066 |
| U.S. | CT-RB | 62.0 | 18.7 | 0.098 |
| U.S. | CT-RB | 133.6 | 24.1 | 0.218 |
| U.S. | CT-RB | 119.1 | 24.8 | 0.143 |
| U.S. | CT-RB | 126.4 | 24.4 | 0.175 |
| U.S. | CT-RB | 146.0 | 26.7 | 0.169 |
| U.S. | CT-RB | 137.6 | 25.2 | 0.146 |
| U.S. | CT-RB | 129.6 | 25.7 | 0.149 |
| U.S. | CT-RB | 133.6 | 24.9 | 0.285 |
| | | | | 0.149 ($\bar{x}$) |
| U.S. | BH | 87.4 | 20.0 | 0.125 |
| U.S. | BH | 57.0 | 17.5 | 0.093 |
| U.S. | BH | 74.2 | 19.6 | 0.100 |
| | | | | 0.103 ($\bar{x}$) |
| B.S. | CT-RB | 77.0 | 20.8 | 0.030 |
| B.S. | CT-RB | 225.1 | 31.5 | 0.067 |
| | | | | 0.049 ($\bar{x}$) |
| B.S. | BH | 59.4 | 17.3 | 0.038 |
| B.S. | BH | 134.8 | 22.6 | 0.068 |
| B.S. | BH | 126.8 | 22.6 | 0.078 |
| B.S. | BH | 88.4 | 19.8 | 0.055 |
| B.S. | BH | 112.6 | 21.6 | 0.059 |
| B.S. | BH | 76.7 | 19.8 | 0.120 |
| B.S. | BH | 94.4 | 20.8 | 0.095 |
| B.S. | BH | 174.6 | 24.9 | 0.093 |
| | | | | 0.076 ($\bar{x}$) |
| B.S. | BC | 47.4 | 15.5 | 0.026 |
| B.S. | BC | 91.8 | 19.1 | 0.048 |
| B.S. | BC | 38.6 | 15.0 | 0.048 |
| B.S. | BC | 69.7 | 17.3 | 0.024 |
| | | | | 0.037 ($\bar{x}$) |
| B.S. | BG | 68.2 | 16.5 | 0.061 |
| B.S. | BG | 69.2 | 16.3 | 0.038 |
| B.S. | BG | 70.5 | 16.3 | 0.061 |
| | | | | 0.053 ($\bar{x}$) |

[a] U.S. = Upper Squaw Lake; B.S. = Big Squaw Lake
[b] CT = Cutthroat trout *Salmo clarki* Richardson
CT-RB = Cutthroat-Rainbow trout cross
RB = Rainbow trout *Salmo gairdneri* Richardson
BH = Brown bullhead *Ictalurus nebulosus*
BC = Black crappie *Pomoxis nigromaculatus*
BG = Bluegill *Lepomis macrochirus*

The rate at which fish assimilate toxicants (*e.g.,* methylmercury) may be accelerated when the fish are stressed by increased temperatures, reduced dissolved oxygen concentration, high pH, or a combination of all three factors (Lloyd, 1961; Warren, 1971). Accordingly, as temperatures rise, the fish may respond with a sudden increase in dissolved oxygen consumption. Increased respiration rates will result in proportionately higher exposure to methylmercury and a consequent higher assimilation of the substance as respiratory surfaces receive larger quantities of mercury-laden water. Likewise, under conditions of low dissolved oxygen, fish may be forced to respire more rapidly to acquire sufficient oxygen. As the quantity of water increases across respiratory surfaces, the fish may be exposed to more methylmercury.

In Upper Squaw Lake, fish may be forced to occupy depths around 5-6 m to avoid less favorable temperatures of the overlaying water. In occupying the 5-6 m stratum, however, the fish are exposed to exceedingly low concentrations of dissolved oxygen, and find themselves compressed between high temperatures and pH above and dangerously low D.O. below. This condition may force an abnormally high number of fish into a narrow band of water resulting in excessive competition for food and space, and predation. Consequently, stress develops which forces abnormally high respiration rates and possible increase in mercury assimilation. Conversely, Big Squaw Lake appears to offer suitable fish habitat from thermocline (*i.e.,* 6-7 m) to 20 m (Table 3). Thus, Big Squaw fish are less likely to encounter temperature, pH, and oxygen-related stress which may account for the lower mercury concentrations found in their tissues.

The higher concentrations of mercury in Upper Squaw Lake sediments may have little relationship to the levels of mercury found in Upper Squaw Lake fish. Langley (1973) showed an inverse relationship between methylation rates and the concentration of mercury in sediments. Methylation rate, according to Langley, was dependent far more on the organic enrichment and microbial density of the sediments rather than on mercury content.

TABLE 2. Mercury content of Squaw Lakes fish (total mercury, wet weight basis) collected 23-24 April 1975. Analyses by U.S. Food and Drug Administration, Seattle, Washington, U.S.A.

| | | 23-24 April | | | |
|---|---|---|---|---|---|
| Lake[a] | Species[b] | Weight (g)[c] | Fork length (cm)[d] | Number fish composited | Mercury conc. (p.p.m.) |
| U.S. | CT | 51-150 | 17.8-25.9 | 8 | 0.68 |
| U.S. | BH | 33 | 14.0 | 1 | 0.52 |
| B.S. | CT-RB | 217-282 | 27.4-30.2 | 5 | 0.31 |
| B.S. | RB | 54-292 | 18.8-29.7 | 14 | 0.32 |
| B.S. | BH | 108-241 | 20.3-26.7 | 2 | 0.29 |
| B.S. | BC | 40-243 | 13.5-24.9 | 26 | 0.26 |
| B.S. | BG | 39- 89 | 11.9-16.3 | 8 | 0.21 |

[a] U.S. = Upper Squaw Lake: B.S. = Big Squaw Lake
[b] CT = Cutthroat trout *Salmo clarki* Richardson
CT-RB = Cutthroat-Rainbow trout cross
RB = Rainbow trout *Salmo gairdneri* Richardson
BH = Brown bullhead *Ictalurus nebulosus*
BC = Black crappie *Promoxis nigromaculatus*
BG = Bluegill *Lepomis macrochirus*
[c] Range of individuals in composite
[d] Range of individuals in composite

TABLE 3. Temperature, pH and dissolved oxygen profiles in Squaw Lakes, Oregon, Summer, 1975. Values for temperature and dissolved oxygen (D.O.) reported in degrees centigrade and milligrams per liter, respectively.

| | Big Squaw | | | | | Upper Squaw | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 25 July | | | 22 August | | 25 July | | | 22 August[a] | | 23 August[b] |
| Depth (m) | Temp. | pH | D.O. | Temp. | D.O. | Temp. | pH | D.O. | Temp. | D.O. | D.O. |
| Surface | 24.2 | 7.9 | 7.7 | 20.4 | 9.3 | 23.6 | 8.9 | 13.1 | 20.6 | 10.5 | 10.2 |
| 1 | 23.6 | | | 19.9 | | 22.1 | | | 19.4 | | |
| 2 | 23.4 | | | 19.9 | | 19.9 | | | 18.9 | | 9.9 |
| 3 | 23.0 | 8.2 | 7.8 | 19.9 | | 18.3 | 9.1 | 14.4 | 18.3 | | |
| 4 | 20.8 | | | 19.9 | 10.7 | 16.4 | | | 17.8 | | |
| 5 | 14.3 | | | 18.2 | | 14.4 | | | 16.7 | | 7.0 |
| 6 | 11.3 | 7.8 | 9.1 | 15.4 | | 13.1 | 8.4 | 10.7 | 16.1 | | 3.1 |
| 7 | 8.5 | | | 11.0 | | 11.9 | | | 13.9 | 2.2 | 0.22 |
| 8 | 7.7 | | | 5.6 | | 10.5 | | | 12.2 | | |
| 9 | 7.1 | 7.6 | 6.7 | 5.4 | | 8.8 | 8.2 | 4.1 | 10.0 | | |
| 10 | 6.8 | | | 4.9 | | 7.8 | | | 8.9 | | |
| 11 | 6.6 | | | 4.9 | 5.9 | 7.4 | | | 8.3 | 0.08 | |
| 12 | 6.4 | 7.6 | 6.8 | 4.9 | | 7.0 | 8.3 | 1.2 | 7.7 | | |
| 13 | 6.2 | | | 4.9 | | 7.0 | | | 6.7 | | |
| 14 | 6.1 | | | 4.9 | | | | | 6.1 | | |
| 15 | 5.9 | 7.5 | 6.8 | 4.9 | | | | | 6.1 | 0.0 | |
| 16 | 5.9 | | | 4.9 | | | | | | | |
| 17 | 5.7 | | | 4.9 | | | | | | | |
| 18 | 5.6 | | | 4.9 | | | | | | | |
| 19 | 5.6 | | | 4.9 | | | | | | | |
| 20 | 5.5 | 7.5 | 6.2 | 4.9 | 5.2 | | | | | | |
| 25 | 5.5 | | | 4.9 | | | | | | | |
| 27 | 5.4 | | | 4.9 | 0.23 | | | | | | |

[a] 1500 hrs.
[b] 0500 hrs.

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## Association News

The annual meeting of the Association was held at Oregon Colloge of Education at Monmouth, Oregon on March 24, 25, and 26. About 300 persons registered for the meeting and some 140 papers were delivered in the various sections. A special symposium on Northwest Coastal Environment: Its Relationship to Man's Use was held on Friday and a second one on the Changing Science Curriculum K-12 was held on Saturday. One preconference field trip and two Saturday field trips were well attended.

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# The Taxonomic Status of Brodiaea howellii Watson, (Liliaceae)

**Abstract**

*Brodiaea howellii* and *B. douglasii* have received varied taxonomic treatment in recent floras. In my study, a combination of morphological, biochemical, and cytological procedures were used to examine the relationship between them. Field and herbarium studies confirmed that reliable morphological criteria exist for distinguishing the two taxa, the most significant being the location and morphology of the inner filaments. Chromatographic studies of inflorescence extracts showed that the two taxa differ both with respect to the compounds present and to the concentration of compounds common to both. The chromosome base number is $x = 8$ in each taxon and the chromosomes of the two are morphologically indistinguishable. In both *B. howellii* and *B. douglasii,* diploids ($2n = 16$), triploids ($2n = 24$), and tetraploids ($2n = 32$) were found. No morphologically intermediate plants were observed in the field, but a few were found among the herbarium specimens examined. The paucity of such specimens, together with the morphological and biochemical distinctiveness of the two taxa, is considered sufficient to warrant their recognition at the specific level.

The taxa here called *Brodiaea howellii* Watson and *B. douglasii* Watson have received varied treatment in recent floras of the Pacific Northwest. Hitchcock *et al.* (1969) regard the two as distinct species; Peck (1941) and Munz (1959) treat them as conspecific varieties, *B. douglasii* var. *howellii* (Watson) Peck, and B. *douglasii* var. *douglasii;* Taylor (1966) does not distinguish between the two taxa, listing only *Triteleia grandiflora* Lindley [=*B. douglasii*] as being present in British Columbia.

The two taxa have a similar latitudinal range but differ in their east-west distribution (Fig. 1). The range of *B. howellii* extends from the eastern slopes of the Cascades to the Puget-Willamette Trough, whereas that of *B. douglasii* extends eastward from the Cascades into Montana and Wyoming. According to Hoover (1955), the two taxa usually occupy different areas but, where they are in proximity, they intergrade.

Watson (1879) originally characterized *B. howellii* as resembling large forms of *B. lactea* Watson [=*B. hyacinthina* (Lindley) Baker] but with purplish flowers, short, deltoid outer filaments, and longer, broadly winged inner filaments that are truncate or rounded above. Greene (1886), Piper (1906), and Abrams (1923) emphasized the resemblance of *B. howellii* to *B. douglasii,* distinguishing between them on the basis of filament characteristics: in *B. douglasii* the inner filaments are short and peglike, the outer filaments long and keeled but not winged.

Hoover (1941), in the only monographic study to include the two taxa, recommended reducing *B. howellii* to varietal status. He stated that the only consistent difference between them was their filament morphology and even this showed some intergradation (Hoover 1941, 1955). Hitchcock *et al.* (1969), however, identified several distinguishing features, many of which had not been reported previously. Among these were the manner of insertion of the filaments, the reflexing and degree of ruffling of the tepals, the length of the pedicels, and length of the perianth tube. These authors also stated that herbarium specimens suggested that a color difference exists between specimens

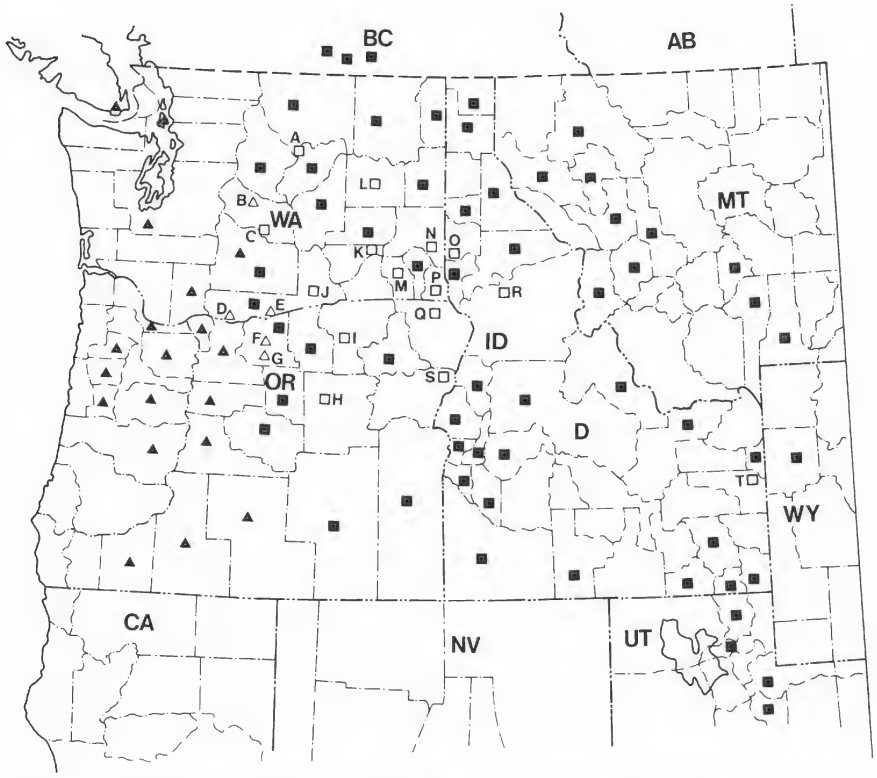


Figure 1. Distribution of *Brodiaea howellii* (▲, △) and *B. douglasii* (■, □) by county and location of sampled populations. Herbarium records, ▲, ■; sampled populations, △, □; Alta Lake, A; Virden, B; Umtanum, C; Wishram, D; Roosevelt, E; Nolex, F; Solex, G; Long Creek, H; Nye, I; Kiona, J; Palouse, K; Rock Lake, L; Tucannon, M; Steptoe, Wawawai, Wawawai 5, N; Troy, O; River-early, River-late, Knoll, Hill, Slope, Ayer Creek, Puffer Butte, Mill Creek, P. Buford Ridge, Q; Kooskia, R; Halfway, S; Rainy Pass, T.

of *B. howellii* from the two sides of the Cascade axis but that they were unable to obtain fresh material to confirm the situation.

A third taxon, *B. bicolor,* was described by Suksdorf (1902) as differing from *B. howellii* in its size, corm and perianth morphology, phenology, and ecology. Hoover (1941), however, concluded that it was merely a color variant of *B. howellii,* not meriting formal taxonomic recognition. Subsequent authors have concurred with Hoover's treatment.

I became interested in the question of the relationship between *B. howellii* and *B. douglasii* during a study of the intraspecific variation in the latter species (Barkworth, 1975). Consequently, I included a few populations of *B. howellii* in my study. Unfortunately, I too was unable to locate any extant populations of *B. howellii* on the west side of the Cascades during the course of the study. Nevertheless, the combination of field, laboratory, and herbarium studies yielded interesting information bearing on the relationship between the two taxa.

## Methods and Materials

*Morphology: Brodiaea howellii* and *B. douglasii* have generally been distinguished by their floral morphology and overall size. Accordingly, I measured various morphological features (Table 1) on samples of up to fifty flowering shoots from several native populations (Fig. 1). The means of these measurements were compared using the *t*-test for unpaired observations and unequal variances (Steel and Torrie, 1960). A second comparison was also made using only the diploid populations of each species. These measurements were supplemented by qualitative observations, both of living material and of herbarium specimens from the following institutions: British Columbia Provincial Museum (V), California Academy of Sciences (CAS), College of Idaho (CIC), Harvard University (A and GH), Idaho State University (IDS), Missouri Botanical Garden (MO), New York Botanical Garden (NY), Oregon State University (OSC), Pomona College (POM), Rancho Santa Ana Botanic Garden (RSA), Stanford University (DS), United States National Herbarium (US), University of Alberta (ALTA), University of California (UC), University of Montana (MONTU), University of Oregon (ORE), University of Washington (WTU), Utah State University (UTC), Washington State University (WS), Western Washington State College (WWB).

*Chromatography:* The sample populations of *B. howellii* had white flowers, sometimes tinged with blue; those of *B. douglasii* were either pale or dark blue. Since flower color is largely determined by flavonoid compounds, methanolic extracts of the inflorescences were examined by two-dimensional descending paper chromatography. Three additional species, *B. hyacinthina, B. laxa* Bentham, and *B. congesta* Smith were included in this portion of the study. The extracts were prepared by drying the inflorescences, grinding them up, five at a time, and soaking the resulting powder in cold methanol (3 ml/gr dry wt or sufficient to cover) for 24-72 hrs. Three samples (0.05, 0.10, 0.15 ml) of each extract were run, using Whatman 3MM paper. The chromatograms were viewed with visible and long wavelength ultraviolet light, both with and without ammonia vapor.

In comparing the chromatograms, I assumed that pigments having the same relative

TABLE 1. Summary of measured morphological characteristics of *Brodiaea howellii* and *B. douglasii*.

| | *B. howellii*[a] | *B. douglasii*[b] |
|---|---|---|
| Leaf length (cm) | (25-62) 40[c] | (26-29) 42 |
| Peduncle length (cm)** | (27-61) 42 | (28-64) 47 |
| Leaf width (mm)** | (2.3-8.7) 4.7 | (3.4-9.1) 6.3 |
| Corm depth (cm) | (5-18) 10 | (4-18) 10 |
| Number of flowers* | (4.9-14.7) 8.9 | (6.1-16.8) 9.9 |
| Pedicel length (cm)* | (0.9-1.6) 1.1 | (0.8-1.7) 1.2 |
| Perianth length (mm)** | (17-22) 18 | (15-25) 20 |
| Perianth tube (mm)** | (9-12) 10 | (8-13) 11 |
| Stipe (mm)** | (1.2-2.1) 1.5 | (1.0-4.4) 2.5 |
| Filament insertion separation (mm) | ca 0.5 | (1.4-3.2) 2.5 |

* *t*-test for difference between means significant at 1 percent level.
** *t*-test for difference between means significant at 0.1 percent level.
[a] Measurements based on plants from five different populations sampled during 1972 and 1973. Three populations were sampled in both years.
[b] Measurements based on plants from 20 different populations sampled during 1972 and 1973. Five populations were sampled in both years.
[c] Numbers given are (lowest population mean-largest population mean) overall mean.

position and visual characteristics were identical. The populations were compared using a weighted similarity index which lessened, without ignoring, the significance of pigments detected in some but not all extracts of a particular population. It was calculated for each pair of populations, A and B, as $S_{AB} = \frac{F_{AC} + F_{BC}}{F_A + F_B}$

where $F_A$ and $F_B$ are the sums of the frequencies, in populations A and B respectively, of pigments present in either or both populations.

$F_{AC}$ and $F_{BC}$ are the sums of the frequencies, in populations A and B respectively, of the pigments common to both populations.

The frequency of a pigment in a population was defined as:

$$\frac{\text{number of extracts of the population which had the pigment}}{\text{total number of extracts prepared from the population}}.$$

$S_{AB}$ reduces to a simple matching coefficient if all pigments are present with a frequency of 100 percent or 0 percent. A phenogram was prepared by single linkage cluster analysis (Sneath and Sokal, 1973).

*Cytology:* Corms collected from the native populations were grown on moist sand in a cool greenhouse. Root tips for cytological analysis were obtained from these corms. The tips were collected around mid-day, and placed in 0.1 percent (w/v) colchicine for 4-6 hrs, hydrolysed in 50 percent HC1, and then squashed and stained in acetocarmine. The coverslips were then ringed with Massarts solution (50g gum arabic, 100 g chloral hydrate, 100 ml water) and the slides allowed to dry at room temperature for 24 hrs before being examined.

#### Results and Observations

*Morphology: B. howellii* and *B. douglasii* were very similar with respect to the measurements that were made (Table 1). Nevertheless, the differences between the means for the two taxa were found to be statistically significant at the 1 percent level or lower for all but leaf length and corm depth. In each instance, the mean for *B. howellii* was lower than that for *B. douglasii.* When only the diploid populations were compared, the differences were statistically significant at the 0.1 percent level for all but corm depth, for which the difference was not significant.

Except in size, the plants of *B. howellii* and *B. douglasii* collected for this study were markedly different. Those of *B. howellii* had creamy white perianths, sometimes tinged with blue, and almost round inner tepals that were smooth and reflexed at approximately the same level as the outer tepals. The inner filaments were wide (2-3mm) and flat, but the outer filaments were often no more than a peglike protrusion from the perianth. Occasionally this peg was located on a base similar in shape to that of the inner filaments but much shorter. The two sets of filaments were attached to the perianth tube at approximately the same level or, at any rate, less than 1.0 mm apart, a distance close to the limits of accuracy in determining the point of insertion and considerably less than the comparable distance in *B. douglasii.*

In *B. douglasii,* the perianths were blue and the inner tepals were oval, strongly ruffled, and generally reflexed 1.5-3 mm above the outer tepals. In one *B. douglassii* population (Rainy Pass) a few plants had a filament separation of 1 mm, but the flowers of all plants in this sample were depauperate, probably as a result of environmental

factors (Barkworth, 1975). In all the *B. douglasii* populations the inner filaments were narrow and thick and were inserted above the peglike outer filaments. The peg was never attached to a basal portion similar to the inner filaments. The stipe of the ovary was usually much shorter in *B. howellii* than in *B. douglasii* (Table 1).

The two taxa were readily distinguished by these floral characters. In addition, the corms of *B. howellii* had more tunic layers made of coarser fibers than observed in *B. douglasii*. The Nye population of *B. douglasii* was exceptional, however, in having "howellii" corms although being typically "douglasii" in all other respects. Suksdorf (1902) mentioned the coarse-fibered corm coat of *B. howellii* as one characteristic separating it from *B. bicolor*.

*Chromatography:* Visual examination of the chromatograms revealed that each of the taxa examined had a distinct chromatographic profile. The relative concentrations of the various compounds were also characteristic for each taxon, but this fact was not considered in calculating the similarity indices.

The populations of *B. howellii* and *B. douglasii* formed separate clusters (Fig. 2) which were, however, more similar to each other than to the other taxa in the study. Of the other three taxa, *B. laxa* is in the same section as *B. douglasii* and *B. howellii; B. hyacinthina* is in the same subgenus but a different section; *B. congesta* is in another subgenus (Munz, 1959).

A total of 32 pigments was detected in *B. douglasii* and *B. howellii*. Ten were restricted to *B. douglasii,* seven to *B. howellii,* and 15 were common to both taxa (Table 2). Two anthocyanin pigments, both delphinidin based (Barkworth, unpublished data) were present in *B. douglasi*. The major one (#3) was also detected in some extracts of *B. howellii,* albeit at a much lower concentration. Both anthocyanins were present in *B. laxa* and *B. congesta*.

The collections of *B. douglasii* included both dark and light blue populations but these did not form separate clusters in the phenogram. Indeed, the first cluster contains two dark blue and one light blue population. Re-examination of the chromatograms did not reveal any differences in pigment concentration that would account for the color difference. Flower color is, however, a function of both the compounds present and their molecular environment (Nakayama and Powers, 1972), both of which are subject to genetic control.

*Cytology:* In both *B. howellii* and *B. douglasii* the basic chromosome number is $x = 8$. Diploid ($2n = 16$) and tetraploid ($2n = 32$) corms of *B. howellii* were found, as well as one triploid ($2n = 24$) (Table 3). A greater range of polyploid levels was observed in *B. douglasii* (Barkworth, 1975), but this observation may reflect merely the larger number of *B. douglasii* populations examined (25 *vs* 4).

The chromosome complements of the two taxa are indistinguishable morphologically (Fig. 3). All the chromosomes in each taxon have subterminal centromeres and, although there are differences in chromosome length within each taxon, the differences are too small to permit recognition of individual chromosomes or groups of chromosomes. Crossing, both within and between taxa, was attempted, but the high failure rate, as measured by seed set, precluded use of these data.

Polyploid plants of *B. douglasii* tend to exhibit "gigas" characteristics and to produce several offsets. Furthermore, they are often ecologically separated from diploid populations, tending to occupy more unstable areas. Too few populations of *B. howellii* were

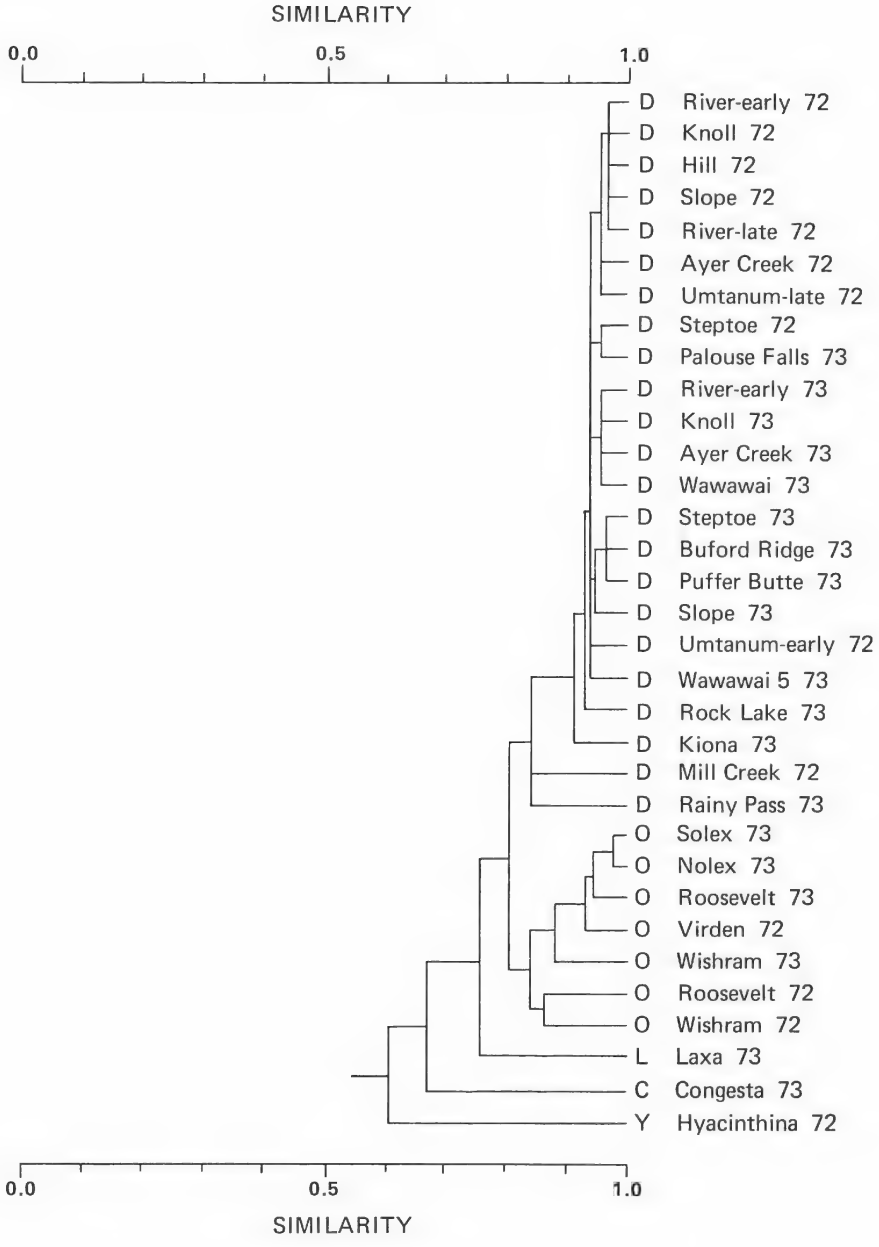


Figure 2. Phenogram based on single linkage analysis of chromatographic data obtained from 33 populations of *Brodiaea*. Samples were collected in 1972 (72) and 1973 (73). The species represented are: *B. douglasii* (D), *B. howellii* (O), *B. laxa* (L), *B. congesta* (C), and *B. hyacinthina* (Y).

TABLE 2. Properties and distribution of pigments detected in five species of *Brodiaea*.

| Compound number | $R_f$ values TBA[c] | HAc[d] | Appearance vis. | vis.-$NH_3$ | uv | uv-$NH_3$ | Occurrence[b] |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 5 | — | — | opi-f | b-opi-f | d,o |
| 2 | 5 | 2 | — | — | opi-f | b-opi-f | d,o,l,c |
| 3 | 8 | 45 | b | b | w | w | d,o,c |
| 4 | 7 | 65 | — | — | opi | opi | d |
| 5 | 8 | 81 | — | — | p | p | d,o,l,c |
| 6 | 31 | 70 | — | — | p | p | d,o,l |
| 7 | 29 | 79 | — | — | lb | gp | d,l |
| 8 | 42 | 67 | — | — | w | — | d,l |
| 9 | 37 | 75 | — | — | opi | opi | l |
| 11 | 65 | 51 | — | y | p | y | d,o,c |
| 12 | 10 | 53 | b | b | w | w | d,l,c |
| 13 | 31 | 76 | — | y | p | y | d,l |
| 14 | 62 | 77 | — | — | p | y | l |
| 15 | 78 | 56 | — | — | — | lb | l |
| 16 | 40 | 14 | — | — | y | cy | d,l |
| 17 | 72 | 69 | — | — | — | lb | l |
| 18 | 26 | 74 | — | y | p | y | c |
| 19 | 40 | 57 | — | y | p | y | d,o,l |
| 20 | 72 | 13 | — | — | b-f | b-b-f | d,o,l,y,c |
| 21 | 79 | 19 | — | — | db-f | db-f | d,o,l,c |
| 22 | 57 | 47 | — | — | p | y | d,y |
| 23 | 77 | 54 | — | — | lb | b-f | d,o,l,y,c |
| 24 | 71 | 42 | — | — | lb | lb | o,l,c |
| 25 | 67 | 59 | — | y | p | y | d,c |
| 26 | 52 | 62 | — | — | p | y | d,o,y |
| 27 | 72 | 4 | — | — | y | y | d,o,l |
| 28 | 56 | 74 | — | — | — | gb | l,y |
| 29 | 28 | 63 | — | — | — | lb | d,y |
| 30 | 68 | 10 | — | — | p | y | c |
| 31 | 34 | 74 | — | — | lb | lb | o,y |
| 32 | 28 | 50 | — | — | p | y | o |
| 33 | 46 | 38 | — | — | lb | lb | d,o |
| 34 | 74 | 31 | — | — | p | p | o |
| 35 | 75 | 61 | — | — | p | y | d,o |
| 36 | 12 | 72 | — | — | p | y | o,y |
| 37 | 55 | 72 | — | — | p | y | d,o,c |
| 38 | 82 | 22 | — | — | p | p | o |
| 39 | 26 | 73 | — | — | p | p | l,c |
| 40 | 82 | 32 | — | — | p | p | o |
| 41 | 65 | 62 | — | — | p | p | v |
| 42 | 65 | 74 | — | — | — | lb | d,c |

[a] b, blue; db, deep blue; f, fluorescent; gb, green-blue; lb, light blue; opi, orange-pink; oy, orange-yellow; p, purple; w, white; y, yellow.

[b] d, *B. douglasii;* o, *B. howellii;* l, *laxa;* y, *B. hyacinthina;* c, *B. congesta.*

[c] Tertiary butanol:acetic acid:water (3:1:1,v/v).

[d] Acetic acid:water (15: 85, v/v).

TABLE 3. Chromosome counts for *Brodiaea howellii.*

| Population | Count |
|---|---|
| Nolex | $2n = 16(3)$[a] |
| Wishram | $2n = 16(1), 32\ (4)$ |
| Virden | $2n = 16(5)$ |
| Roosevelt | $2n = 24(1)$ |

[a] Number of corms counted.

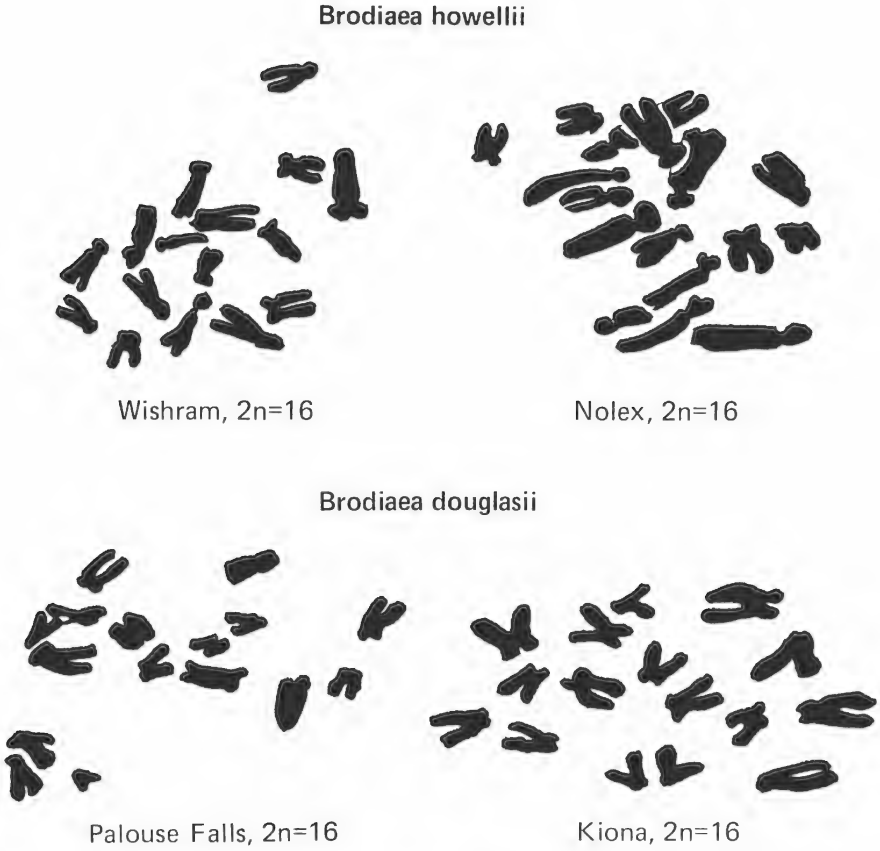


Figure 3. Mitotic chromosomes of *Brodiaea douglasii* and *B. howellii.*

examined to generalize concerning the situation in this taxon. The Wishram population, which was the only one in which tetraploid corms were observed, also contained the largest plants observed. It was, however, located on deep soil near the bottom of a south facing slope and was protected from grazing. The other populations were all growing in rocky soil and heavily grazed areas. The fact that the differences between the means were statistically more significant when just the diploid populations of the two species were compared suggests that in *B. howellii* as in *B. douglasii,* polyploidy is associated with an increase in size. This association may, however, be a function of the sample used, for only two populations (one of which was represented by collections from both 1972 and 1973) of *B. howellii* were diploid. None of the *B. howellii* populations produced large numbers of offsets either in the field or in the greenhouse.

**Discussion**

As exemplified by the populations sampled, *B. howellii* and *B. douglasii* are two quite distinct taxa, easily distinguished by their floral characteristics. Moveover, chromatography revealed that the two taxa have very distinct pigment complements in addition

to having different concentrations of the compounds common to both taxa. The distinguishing features are, however, often obscure in herbarium specimens, forcing one to rely on filament width and insertion in making determinations.

No live plants and very few herbarium specimens were found that seemed to be intermediate between the two taxa in their morphology. Since species of *Brodiaea* are perennial herbs capable of vegetative reproduction, the paucity of intermediate specimens, particularly in the region where both taxa are found, is surprising and suggests that gene flow between the two is, at best, extremely limited.

Some variation within *B. howellii* was suggested by the herbarium specimens. Plants from western Washington and southern Vancouver Island appear to have been blue, as are those of *B. douglasii.* Those from Vancouver Island were also somewhat intermediate in their filament characteristics: the distance between the insertion of the upper and lower filaments was as much as 1.0 mm, rather more than usual for *B. howellii,* and the filament width was around 1.5 mm, rather narrower than usual for that species. The plants from western Washington were typically "howellii" in these respects. Flowers of *B. howellii* often turn somewhat blue after anthesis or during drying, but such color is usually not as intense nor as evenly distributed as in *B. douglasii.* That the plants on Vancouver Island are blue in life is shown by a photograph in "Wild Flowers of Field and Slope" (Clark, 1974) which was taken in Beacon Hill Park, Victoria, B.C. (personal communication). This photograph also shows that the filaments are flat as is characteristic of *B. howellii.* It appears, therefore, that apart from their perianth color, plants from western Washington and southern Vancouver Island fall well within the bounds of the "howellii" taxon.

The taxonomic status of *B. howellii* and *B. douglasii* is, of course, ultimately a matter of subjective judgment. Nevertheless, in view of their morphological and biochemical distinction and the lack of evidence for gene exchange between them, I recommend that the two taxa be treated as separate species, *B. howellii* and *B. douglasii,* separable as follows:

Inner filaments narrow (ca 1mm), keeled, inserted (1.0) 1.4-3.5 (5.0) mm above the outer filaments; inner tepals strongly ruffled, particularly at base, reflexed approximately 2 mm above the outer tepals; perianth pale to dark blue; stipe (0.5) 1.0-4.4 (6.0) mm; tunic of corm fine-fibered ..... *B. douglasii;*
Inner filaments wide (2-3 mm), flat, inserted 0-0.5 (1 mm) above the outer filament; inner tepals scarcely ruffled, reflexed at same height as outer tepals; perianth usually creamy white, sometimes tinged with blue particularly after anthesis, occasionally blue all over; stipe 1.2-2.1 (2.5) mm; tunic of corm coarse-fibered ..... *B. howellii.*

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# Vegetation Patterns on Limestone and Acid Parent Materials in the Garnet Mountains of Western Montana[2]

**Abstract**

Parent material has a strong influence on the distribution and coverage provided by individual species and life forms. *Pinus contorta* var. *latifolia* and the *Vaccinium* species, in particular, are poorly represented over limestone substrates. Classification of the vegetation on each substrate by habitat types also reveals marked differences. Nomenclature follows that of Hitchcock and Cronquist 1973, except where authorities are given.

## Introduction

Parent material plays a major role in the development of a soil and its physical and chemical properties. Limestone materials have a particularly significant influence on soil morphology which results from their high base saturation and calcium content, their tendency to produce alkaline soils, and their solubility in weak acids. Because soil is the medium in which most plants grow, parent material influences their growth and distribution.

The objective of this research was to quantify the differences in plant communities on soils developed from limestone as compared to those on granite and quartzite. Particular attention was paid to the distribution of *Pinus contorta* var. *latifolia,* an important tree species in the northern Rocky Mountains, and the *Vaccinium* species.

The influence of parent material on soil properties often causes abrupt differences in vegetal cover and growth rates between adjacent soils formed from different rocks (Bamberg and Major, 1968). Differences have been shown to be particularly evident on serpentine and limestone soils[3] in contrast to soils formed from acid rocks, such as granite (Whittaker *et al.,* 1954; Mooneye *et al.,* 1962; Whittaker and Niering, 1968). The literature pertains almost exclusively to trees. The effects of parent material on undergrowth plants and life forms are scarcely mentioned. No studies have been published on the forest vegetation of limestone soils in western Montana.

Some tree species, such as *Juniperus scopulorum* in the western United States and *J. virginiana* in the Southeast, are associated with and are very tolerant of soils derived from limestone bedrock (Lutz and Chandler, 1946). *Pinus contorta* in the western

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[2] This study was supported by a grant from the Montana Forest Conservation Experiment Station, University of Montana, Missoula, Montana.

[3] For the sake of brevity, the following expressions will be considered synonymous in this report: soils derived from limestone bedrock, limestone soils, limestone-derived soils. Similarly for limestone vegetation, which corresponds to vegetation growing on soils derived from limestone bedrock.

United States and *Quercus robur* L. on the British Isles, on the other hand, are poorly represented on these soils; *Pseudotsuga menziesii* var. *glauca* and *Fraxinus excelsior* L., respectively, generally replace them in the plant community overlying this substrate (Eyre, 1963; Holdorf, 1976).

In the Big Horn Mountains of Wyoming, *Pinus contorta* is clearly associated with granitic substrates and rarely occurs on limestone, whereas the reverse is true with *Pseudotsuga menziesii* (Despain, 1973). A similar relationship between vegetation and substrate is noted by Patten (1963) in the Madison Range of Montana where *Pseudotsuga menziesii* is associated with limestone formations and *Pinus contorta* with volcanic rocks. In Gunnison County, Colorado, Langenheim (1962) reports that *Pinus contorta* occurs only on granitic or coarse clastic parent materials and infrequently on limestone.

Soil chemical and physical factors (especially those related to moisture and phosphorus deficiency) have been reported to be possible causes for species-substrate relationships. The reasons for different species tolerances of limestone and nonlimestone soils, however, are complex and incompletely understood (Goldin, 1976).

### Description of Study Area

The study area encompasses about 2600 ha of forest land in the northwestern part of the Garnet Mountains (lat. 45°50′N, long. 113°20′W) in western Montana about 50 km east of Missoula (Fig. 1).

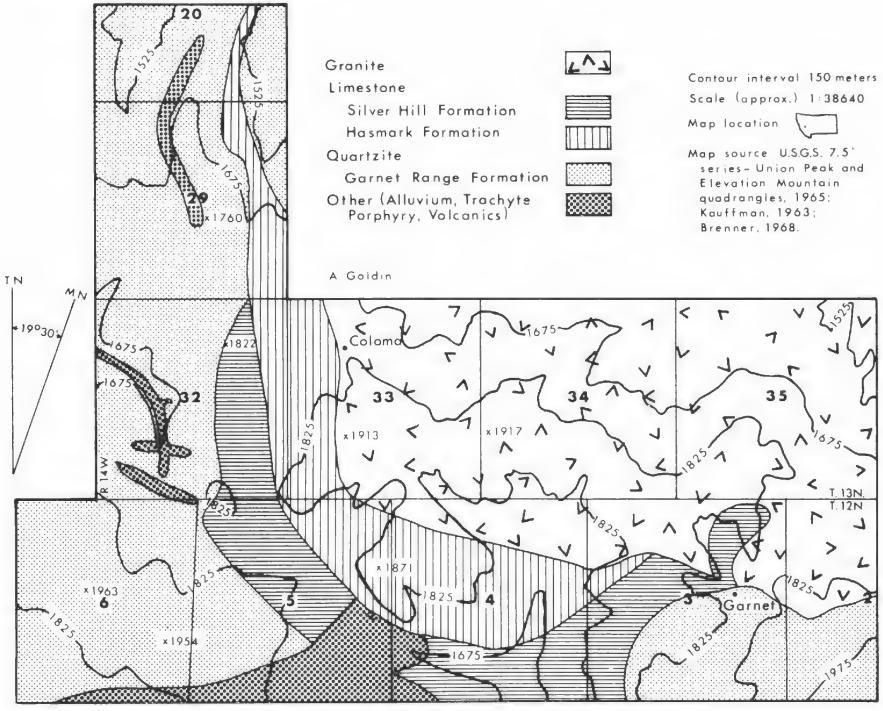


Figure 1. Map of the study area.

Three types of materials underlie the study area: igneous rocks of granite and granodiorite stocks; Cambrian limestones, dolomites, and marbles of the Silver Hill and Hasmark Formations; and Precambrian micaceous quartzites of the Garnet Range Formation (Kauffman, 1963; Brenner, 1968).

The area has a mean annual temperature of about 2°C. Average annual precipitation is approximately 60 cm, which occurs mostly as snow between October and May.

A mosaic of vegetation has resulted from disturbance factors (fire, logging, mining) and site factors (topographic differences and geologic material). The range of vegetational composition extends from the dry *Pseudotsuga menziesii* habitat types on drier slopes over limestone parent material to the temperate, moist *Abies lasiocarpa* habitat types on granite and quartzite (Pfister *et al.,* 1974).

**Methods**

*Plot establishment*: General plot locations on the three substrates were predetermined onto topographic maps based on the following three topographic factors: aspect, elevation, and slope steepness. These locations were determined by stratified random selection from geologic maps (Kauffman, 1963; Brenner, 1968), and the 7.5 minute Union Peak and Elevation Mountain United States Geological Survey topographic maps.

Due to the variability in landscape and the lack of complete constancy of these factors, two aspect groupings, three elevational ranges, and three slope steepness categories were established for each parent material. The interaction of these three factors produced 18 combinations for each substrate. However, since no limestone was present on south slopes below 1675 m on the study area, no data were collected on any parent material in this aspect-elevation grouping. The sample number on each substrate was thus reduced to 15 and the total number of plots to 45.

Ground checking during the summer of 1975 more accurately located the plot centers from the approximate map locations. Once situated at the approximate position, a random and representative sample plot center was established with special precautions to avoid edge effects, obvious ecotones and microsites, dense clumping, and obvious disturbance.

*Field procedures*: The general field procedures for vegetational sampling and habitat classification follow those of Pfister *et al.* (1974). On each 375-$m^2$ circular plot the following data were recorded: 1) location, 2) aspect, 3) elevation, 4) slope steepness, 5) canopy coverage class for tree species in two diameter groupings 10 cm or more at breast height (1.4 m), and those less than 10 cm, and 6) canopy coverage class for each vascular undergrowth plant species. Coverage classes for trees and undergrowth vegetation are as follows:

| Coverage Class | Percentage of Area Covered |
|---|---|
| T | 0-1 |
| 1 | 1-5 |
| 2 | 5-25 |
| 3 | 25-50 |
| 4 | 50-75 |
| 5 | 75-95 |
| 6 | 95-100 |

A soil pit was dug near the center of each plot and described according to standard procedures (Soil Survey Staff, 1951). Color notation followed the Munsell system. Samples of each horizon from six pits, which represented the model profile by aspect on each substrate, were analyzed for particle-size distribution by the hydrometer method (Bouyoucos, 1951), and for the percentage of rock fragments (larger than 2 mm).

*Office procedures:* Association between species on each substrate was determined using the Student's t-test at the 95 percent significance level. The analysis of variance (F-test) was used to test the homogeneity of variance prior to conducting the t-test.

An Index-of-Similarity ordination was constructed to array the stands graphically based on the coverage class values for each plant species (Bray and Curtis, 1957). Most of the meaningful variation was accounted for in the x-axis, which was strongly related to the effects of substrate on vegetational composition. The y-axis was apparently weakly related to temperature. The stands, their habitat types, and the coverage class distribution of the prominent species were plotted on this ordination. End stands for the x-axis, a *Pseudotsuga menziesii/Calamagrostis rubescens* habitat type on limestone, and an *Abies lasiocarpa/Linnaea borealis* habitat type on granite were chosen on the basis of 96 percent dissimilarity and relatively low total dissimilarities with the other stands, indicating that they were not highly unusual.

## Results

*Soils:* The topographic criteria established for plot selection (aspect, elevation, and slope steepness) were subordinate in influence to parent material, which played the major role in the soil development process.

*Limestone:* The soils derived from limestone bedrock were medium-textured, gravelly, calcareous, and neutral to mildly alkaline. Three-fourths of these soils were classified in the Inceptisol order (Typic Cryochrepts); the rest were Entisols (Typic Cryorthents). A summary of the principal differences in soil properties among the three substrates is presented in Table 1.

TABLE 1. Summary of key morphological features of limestone, granite, and quartzite soils in the Garnet Mountains, Montana, based on 15 soil profiles described on each substrate.

| Morphological feature | Substrate | | |
|---|---|---|---|
| | Limestone | Granite | Quartzite |
| Average organic horizon thickness (cm) | 2.3 | 4.0 | 4.0 |
| Common horizon sequences | 01-A1-B2-Cca<br>01-A1-Cca | 01-A1-C<br>01-Bir-C<br>01-Bir-IIA2-C | 01-A2-B2-C<br>01-A1-C<br>01-A2-Bir-C |
| Texture | silt loam | sandy loam | loam |
| Gravel content | gravelly to very gravelly | slightly gravelly | very gravelly |
| Soil reaction (solum) | neutral to mildly alkaline 6.5 - 8.0 | medium to slightly acid 5.5 - 6.5 | slightly acid to neutral 5.7 - 6.9 |
| Calcareousness | Slight to strong on surface; strong at depth | none | none on surface; slight to strong at depth on some profiles |

The organic horizon was significantly thinner on limestone-derived soils than on the soils from the other two substrates. The difference may result from the stimulative effect which calcium carbonate has on the decomposition of plant residues by maintaining alkaline soil conditions suitable for bacterial activity.

A modal limestone soil is described below. Most of the other soils described on this substrate had more rock fragments in the A1 horizon. Some of the profiles were more strongly calcareous near the surface and were thus more alkaline.

TYPIC CRYOCHREPT: LOAMY SKELETAL, MIXED CALCAREOUS, FRIGID
Habitat type: *Pseudotsuga menziesii/Calamagrostis rubescens*
Elevation: 1870 meters Aspect: 340°W Slope: 22 percent

| *Horizon* | *Depth (cm.)* | *Description* |
|---|---|---|
| 01 | 2 - 0 | Decomposed forest litter from *Pseudotsuga menziesii* and undergrowth plants. |
| A1 | 0 - 10 | Very dark brown (10YR 2.5/2) silt loam (5 percent gravel, 22 percent sand, 54 percent silt, 24 percent clay), dark grayish brown (10YR 4/dry); weak moderate granular breaking to weak fine blocky structure; soft, very friable, slightly sticky, slightly plastic; abundant fine roots; neutral (pH 6.8); very slightly calcareous; abrupt boundary. |
| B21 | 10 - 23 | Light olive brown (2.5Y 5.5/4) very gravelly loam (53 percent gravel, 34 percent sand, 48 percent silt, 18 percent clay), yellowish brown (10YR 5/4, dry); weak medium blocky structure; soft, very friable, slightly sticky, slightly plastic; abundant fine roots; mildly alkaline (pH 7.4); slightly calcareous; clear boundary. |
| B22 | 23 - 38 | Dark brown (10YR 4/3) gravelly silt loam (41 percent gravel, 40 percent sand, 51 percent silt, 9 percent clay), brown (10YR 5/3 dry); weak medium blocky structure; soft, very friable, slightly sticky, slightly plastic; common fine roots, mildly alkaline (pH 7.7); strongly calcareous; clear, irregular boundary. |
| Cca | 38 - 93+ | Pale brown (10YR 6/3) gravelly sandy loam (44 percent gravel, 63 percent sand, 26 percent silt, 11 percent clay), very pale brown (10YR 7/3, dry; massive; soft, very friable, slightly sticky, slightly plastic; few roots; moderately alkaline (pH 8.0); strongly calcareous. |

*Granite:* Soils derived from granite were coarse-textured with scattered cobbles, noncalcareous, and of medium acidity. The granitic soils were classified as Entisols (Typic Cryorthents) and Inceptisols (Andic Cryochrepts). These two groups were very similar, differing mainly in the surface mineral horizon, which was a Bir in the Inceptisols and an A1 (ochric epipedon) in the Entisols. A thin, incipient A2 horizon overlaid most of the Bir horizons.[4]

A modal granitic soil is described below. In comparison to this profile, most of the granitic soils had a lower pH, a slightly thinner organic horizon, and a higher percentage of rock fragments.

ANDIC CRYOCHREPT: SANDY SKELETAL, MIXED, FRIGID
Habitat type: *Abies lasiocarpa/Linnaea borealis*
Elevation: 1820 meters Aspect: N10°W Slope: 9 percent

| *Horizon* | *Depth (cm.)* | *Description* |
|---|---|---|
| 01 | 8 - 0 | Decomposed forest litter from *Abies lasiocarpa, Pinus contorta,* and *Pseudotsuga menziesii* and undergrowth plants. |
| Bir | 0 - 31 | Dark brown (7.5YR 4/4) sandy loam (20 percent gravel, 60 percent sand, 31 percent silt, 9 percent clay), brown (10YR 5/3, |

[4] Different professional opinions exist regarding horizon nomenclature and soil classification of these volcanic ash soils. The one used here is in general usage in western Montana at this time.

| | | |
|---|---|---|
| | | dry); weak fine subangular blocky structure, very soft, very friable, slightly sticky, slightly plastic, abundant fine roots; slightly acid (pH 6.5); clear, irregular boundary. Sporadic A2 horizon about 0.5 cm thick occurs above the Bir. |
| C | 31 - 51+ | Brown (10YR 5/3) gravelly coarse sandy loam (25 percent gravel, 72 percent sand, 18 percent silt, 10 percent clay), light brownish-gray (10YR 6/2, dry); massive; loose, very friable, nonsticky, nonplastic; few roots; neutral (pH 6.6). |

*Quartzite:* The quartzitic soils were generally intermediate in morphology between the two soil types above: medium texture, very gravelly, generally noncalcareous, and slightly acidic. Two profiles were recognized on the quartzitic soils: 1) Inceptisols (Typic Cryochrepts) and Entisols (Typic Cryorthents) on the south slope and the drier north slope plots with a 01-A1(ochric)-C horizon sequence on the Entisols and an 01-A2-B2-C on the Inceptisols; and 2) Inceptisols (Andic Cryochrepts) on the moist north slope sites with an 01-A2(incipient)-Bir-C horizon sequence.

Soils of the first type were somewhat similar in description to the limestone soil above except for the noncalcareousness, loam texture, lighter colors, and more gravelly nature of the quartzitic soils. Soils of the second type were like the granitic profile above except for the finer texture and more gravelly nature of the quartzitic soils.

#### Vegetation

The vegetation on soils derived from limestone bedrock was in sharp contrast with that on granitic and quartzitic parent materials. The most obvious differences occurred in the distribution of the following species: *Pseudotsuga menziesii, Pinus contorta, Abies lasiocarpa, Vaccinium globulare, V. scoparium, Linnaea borealis, Xerophyllum tenax,* and *Calamagrostis rubescens.* Intersubstrate relationships were also contrasting in the coverage provided by each life form, in the relative canopy coverage, and in the habitat types associated with each substrate. The plant communities on limestone and granite displayed the greatest dissimilarity. They had no habitat types in common, and there was a wide separation in the ordination of the stands on these substrates (Tables 2, 3, and 4).

The vegetation on quartzite covered almost the entire range of habitat types and of the ordination. The more mesic sites corresponded to those on granite; those on dry sites were similar to ones on limestone.

*Limestone:* The overstory vegetation on the limestone substrate was dominated almost exclusively by *Pseudotsuga menziesii,* providing 34 percent relative coverage. This species generally occurred in open stands and accounted for over 99 percent of the tree coverage.

Shrubs constituted a very minor percentage of the floristic composition on limestone, accounting for only 7 percent relative coverage. Only two species were somewhat important: *Berberis repens* and *Symphoricarpos albus. Vaccinium globulare* and *V. scoparium* played negligible roles in the community structure compared to their roles in the granitic and quartzitic plant communities.

The forb component of the vegetation was a significant part of the limestone plant community, particularly in species diversity. Only two of the 51 forb species found in the study area were absent from limestone soils. In comparison, 37 forbs were found on quartzite and only 20 on granite. The forbs occupied almost one-third of the relative coverage on limestone. The principal forbs were in order of decreasing abundance:

*Arnica latifolia, Aster conspicuus, Thalictrum occidentale, Arnica cordifolia,* and *Antennaria racemosa.*

The graminoids covered over one-fourth of the limestone plots with *Calamagrostis rubescens* composing over 90 percent of this fraction (Figure 2).

The habitat types on limestone were generally the driest in the study area. These

TABLE 2. Relative canopy coverage of important species, including t-statistic, by substrate in the Garnet Mountains, Montana.

| Species | Relative Coverage (percent) | | | t-test significance (95 percent level) | | |
|---|---|---|---|---|---|---|
| | Limestone | Granite | Quartzite | L - G+ | L-Q | G - Q |
| *Pseudotsuga menziesii* | 34 | 12 | 21 | * | * | * |
| *Pinus contorta* | 0 | 18 | 8 | * | * | * |
| *Abies lasiocarpa* | 0 | 8 | 3 | * | * | |
| TOTAL TREES (6) | 34 | 42 | 33 | | | |
| *Arctostaphylos uva-ursi* | — | 4 | 1 | * | * | * |
| *Berberis repens* | 2 | 0 | 1 | * | | |
| *Linnaea borealis* | 1 | 8 | 1 | * | | * |
| *Symphoricarpos albus* | 2 | — | 1 | * | | |
| *Vaccinium globulare* | 1 | 9 | 16 | * | * | |
| *Vaccinium scoparium* | — | 14 | 6 | * | * | * |
| TOTAL SHRUBS (22) | 7 | 39 | 27 | | | |
| *Antennaria racemosa* | 4 | 0 | 1 | * | | |
| *Arnica cordifolia* | 4 | 1 | 1 | * | | |
| *Arnica latifolia* | 7 | 3 | 6 | | | |
| *Aster conspicuus* | 6 | 0 | 1 | | | |
| *Thalictrum occidentale* | 4 | 0 | 1 | * | * | |
| *Xerophyllum tenax* | 0 | 9 | 9 | * | * | |
| TOTAL FORBS (51) | 33 | 15 | 25 | | | |
| *Calamagrostis rubescens* | 23 | 2 | 14 | * | | * |
| *Carex geyeri* | 2 | 1 | 0 | | | |
| TOTAL GRAMINOIDS (6) | 25 | 3 | 15 | | | |
| GRAND TOTAL (85) | 99 | 99 | 100 | | | |

+L = Limestone, G = Granite, Q = Quartzite

TABLE 3. Relative coverage and species diversity according to life form on soils derived from limestone, granite, and quartzite in the Garnet Mountains, Montana.

| Substrate | Life Form | | | | |
|---|---|---|---|---|---|
| | Trees | Shrubs | Forbs | Graminoids | TOTAL |
| LIMESTONE | | | | | |
| Relative coverage (percent) | 34 | 7 | 33 | 25 | 99 |
| Number of species | 3 | 13 | 49 | 6 | 81 |
| GRANITE | | | | | |
| Relative coverage (percent) | 42 | 39 | 15 | 3 | 99 |
| Number of species | 5 | 14 | 20 | 4 | 43 |
| QUARTZITE | | | | | |
| Relative coverage (percent) | 33 | 27 | 25 | 15 | 100 |
| Number of species | 6 | 16 | 37 | 4 | 63 |

were principally *Pseudotsuga menziesii/Calamagrostis rubescens* with some plots classified as *P. menziesii/Symphoricarpos albus* and one as *P. menziesii/Carex geyeri.*

*Granite:* The vegetation on granite was composed of species characteristics of more mesic sites. The most prominent tree species was *Pinus contorta,* although *Pseudotsuga menziesii* and *Abies lasiocarpa* were also important. Of the three substrates, granite had the greatest relative tree coverage (42 percent).

The shrubs accounted for 39 percent relative coverage. The principal ones were *Vaccinium scoparium* and *V. globulare. Linnaea borealis* was also a dominant subshrub.

The forbs and graminoids played a minor role in the floristic composition on granitic soils. Together, they constituted about one-fourth of the relative coverage. *Xerophyllum tenax* and *Calamagrostis rubescens* were the prominent nonwoody plants.

The total amount of coverage was greater on granite than either quartzite or limestone (Goldin, 1976). The habitat types were in the *Abies lasiocarpa* series or the colder part of the *Pseudotsuga menziesii* series*(P. menziesii/Xerophyllum tenax).*

*Quartzite:* Coverage of each life form on quartzite was intermediate between the values on granite and limestone. *Pseudotsuga menziesii* and *Pinus contorta* were the dominant trees, and *Vaccinium globulare* and *V. scoparium* were the principal shrubs.

Forbs produced a relative coverage of 25 percent and graminoids 15 percent. *Xerophyllum tenax, Arnica latifolia,* and *Calamagrostis rubenscens* were the dominant plants in these groups.

Seven of the eight habitat types found in the study area were present on quartzite.

*Ordination of stands*: The Index-of-Similarity ordination indicated marked differences between limestone and granite. Limestone stands were clustered and isolated in the apparently dry section of the ordination while granite was associated with a similar pattern on the moist sites. The stands on these substrates were widely separated. The quartzite stands, on the other hand, were distributed throughout the ordination, but skewed toward the moist end (Figures 3 and 4).

The clustering indicates a relative homogeneity in stand structure on limestone and granite which was entirely absent on quartzite, probably as a result of the greater variability in the soil or quartzite parent rock. The distribution of habitat types also shows a general clustering.

The general sequence of prominent species from the dry limestone sites to the moist granitic sites based on abundance was the following: *Aster conspicuus, Calamagrostis rubescens, Thalictrum occidentale, Linnaea borealis, Arctostaphylos uva-ursi, Xerophyllum tenax, Vaccinium globulare, Pinus contorta, Vaccinium scoparium,* and *Abies lasiocarpa. Pseudotsuga menziesii, Antennaria racemosa,* and *Arnica latifolia* seemed to be

TABLE 4. Habitat type distribution on soils derived from limestone, granite, and quartzite in the Garnet Mountains, Montana.

| Habitat Type (Pfister *et al.*, 1974) | Limestone | Granite | Quartzite |
|---|---|---|---|
| *Pseudotsuga menziesii/Carex geyeri* | 1 | | |
| *P. menziesii/Calamagrostis rubescens* | 11 | | 3 |
| *P. menziesii/Symphoricarpos albus* | 3 | | 1 |
| *P. menziesii/Vaccinium globulare* | | | 1 |
| *P. menziesii/Xerophyllum tenax* | | 2 | 3 |
| *Abies lasiocarpa/Linnaea borealis* | | 9 | 2 |
| *A. lasiocarpa/Xerophyllum tenax* | | 3 | 3 |
| *A. lasiocarpa/Menziesia ferruginea* | | 1 | 2 |

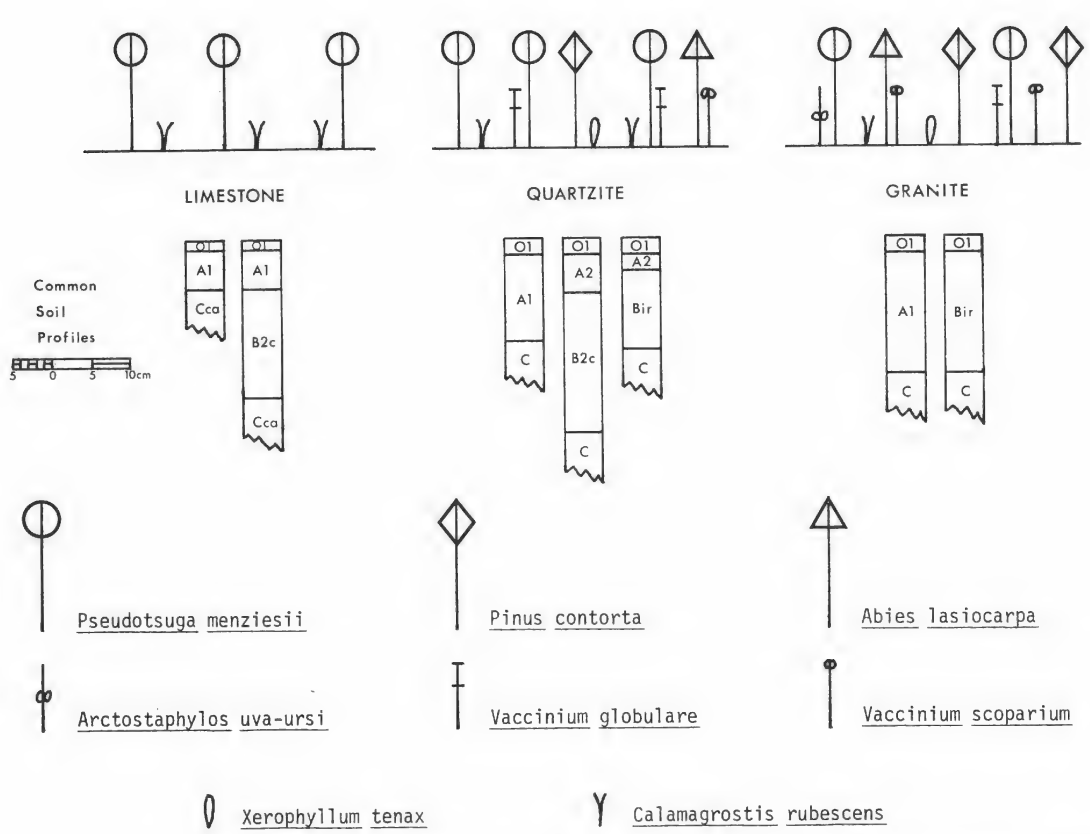


Figure 2. Vegetation patterns and common soil profiles on limestone, quartzite, and granite in the Garnet Mountains, Montana.

fairly well-distributed on all sites. Most of the differences in species distribution probably resulted from parent material differences; some effect may have been caused by minor random differences in the stage of plant succession (Goldin, 1976).

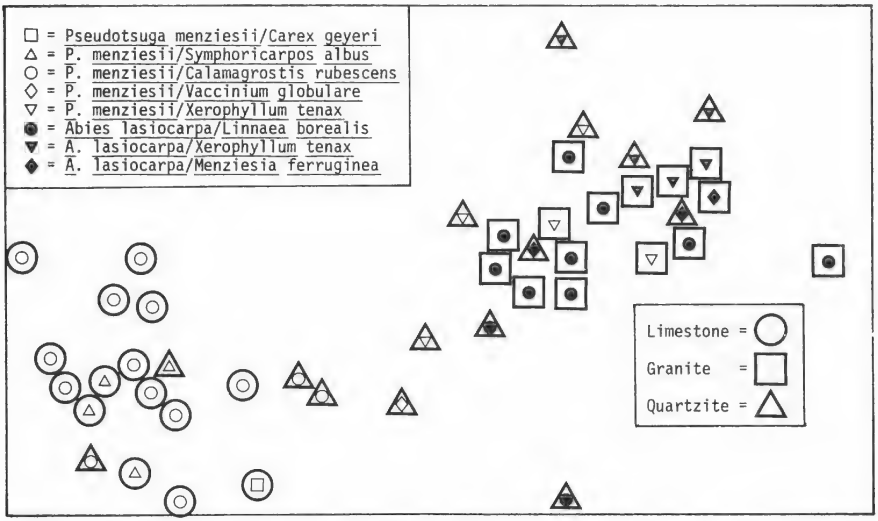
□ = Pseudotsuga menziesii/Carex geyeri
△ = P. menziesii/Symphoricarpos albus
○ = P. menziesii/Calamagrostis rubescens
◇ = P. menziesii/Vaccinium globulare
▽ = P. menziesii/Xerophyllum tenax
● = Abies lasiocarpa/Linnaea borealis
▼ = A. lasiocarpa/Xerophyllum tenax
◆ = A. lasiocarpa/Menziesia ferruginea
Limestone =
Granite =
Quartzite =

Figure 3. Ordination of stands on soils derived from limestone, granite, and quartzite in the Garnet Mountains, Montana.

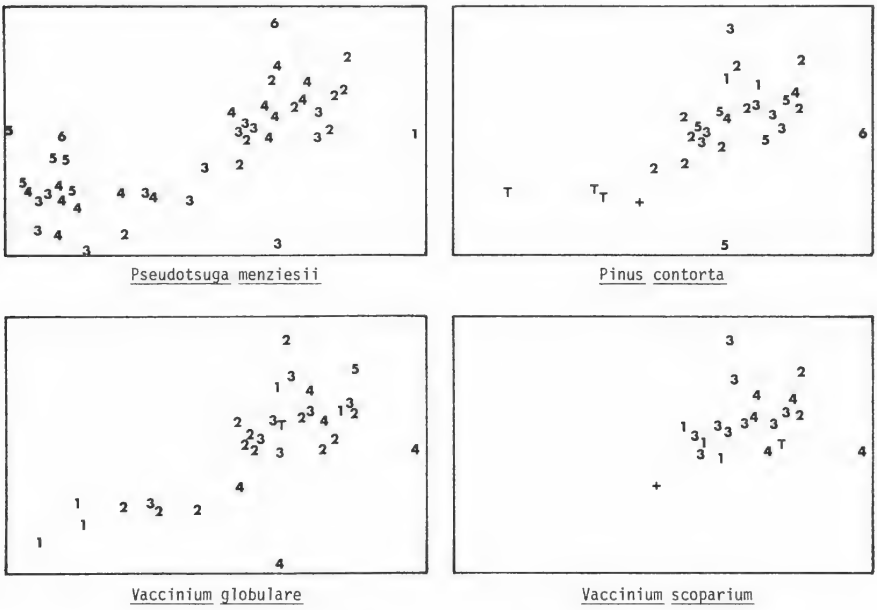


Figure 4. Ordination of individual species in stands on soils derived from limestone, granite, and quartzite in the Garnet Mountains, Montana (numbers indicate coverage classes).

## Discussion

This study shows that definite differences occur in plant distribution and community structure according to the underlying substrate. While a detailed examination of soil moisture was not a part of this research, it appears that the distribution of plant species can be explained, at least in part, from the variations in this factor.

The unpublished theory of Herbert Holdorf (1976) for plant distribution on soils underlain by limestone bedrock in the Little Belt Mountains of Montana is based on observations of soil moisture effects resulting from differences in rock permeability. According to Holdorf, fractures in most limestone bedrock provide more continuous channels for water percolation than are found in either granite or quartzite, which are much more impermeable. Therefore, gravitational water remains longer in soils formed in the latter rocks, thereby delaying the period of drought. On limestone soils, water depletion begins immediately after snowmelt. Holdorf therefore considers limestone soils drier than soils formed in the other rocks, which results in a distinctive and more xeric plant community.

*Pinus contorta* has been found to occur on limestone soils where soil moisture is augmented by higher precipitation or impeded drainage (Goldin, 1976). This species has also been associated with calcareous glacial materials in Montana where drainage is impeded by impermeable rocks underlying the glacial debris (Holdorf, 1976). However, moisture itself may not be the only factor limiting its distribution, since this species can occur on both very wet and very dry sites. For shallow-rooted plants, such as the *Vaccinium* species or tree seedlings, the surface pH may be the key factor to plant distribution (Holdorf, 1976).

Much of the above discussion concerning the key role of soil moisture in plant distribution on limestone soils is speculative. This influence, however, is probably significant enough to warrant research on the soil moisture regime on soils underlain by limestone relative to those formed in acid materials.

## Summary

On limestone and quartzite the dominant tree species was *Pseudotsuga menziesii;* on granite that position was held by *Pinus contorta. Pinus contorta* and *Abies lasiocarpa* rarely occurred on limestone. In the few areas where these species were found on limestone, some soil or topographic feature was present which probably resulted in an augmented moisture content. Thus, the data from this study and observations by field soil scientists suggest that the causative factor for the distribution of *Pinus contorta* and *Abies lasiocarpa* relates to the soil moisture regime.

Shrubs, particularly *Vaccinium globulare* and *V. scoparium,* provided negligible coverage in the plant communities over limestone bedrock, although they were abundant on the other substrates. The dominant shrubs on limestone *(Berberis repens* and *Symphoricarpos albus)* were absent or nearly so on granite and quartzite.

The dominant forb on granite and quartzite was *Xerophyllum tenax* and on limestone, *Arnica latifolia.* The former was rarely present on limestone; the latter occurred on all substrates.

*Calamagrostis rubescens* was the principal graminoid on all three substrates, although it was most prominent on limestone.

The greatest total species diversity occurred on limestone soils and the least on granite. Even though granite had only about half of the species diversity as limestone,

it had greater total coverage than either limestone or quartzite. The coverage of each life form was very different, however. Granite was highest in tree and shrub coverage and lowest in forb and graminoid coverage. Limestone was highest in forb and graminoid coverage, lowest in shrub coverage, and high in tree coverage. Quartzite was intermediate in coverage values among all life forms.

Classification of the vegetation on each substrate by habitat types revealed marked differences, with limestone supporting the driest habitat types, granite the moistest, and quartzite the entire range.

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# A 20-Year Record of Shrub Succession in Logged Areas in the Cedar-Hemlock Zone of Northern Idaho

## Abstract

A record of succession following logging on three sites in hemlock/pachistima *(Tsuga heterophylla/ Pachistima myrsinites)* and two in grand fir/pachistima *(Abies grandis/P. myrsinites)* habitat types in the Coeur d'Alene River drainage of northern Idaho extending over a 14-25-year period is reported. The tall shrub union, over 1 m tall, dominated by *Ceanothus velutinus* on hemlock/ pachistima sites, reached maximum development 3-5 years following logging and burning, and 15-25 years following logging without burning. Tall shrub unions on grand fir/pachistima sites which were logged and burned developed rapidly, and became dominated by *Ceanothus sanguineus;* but subsequent changes were slower than on hemlock/pachistima sites.

## Introduction

Evaluations of vegetation composition on five different sites in the Coeur d'Alene River area of northern Idaho have provided a record of succession following clearcutting that extends over approximately a 20-year period (Table 1). These sites were described by Pengelly (1961, 1963, 1966) in 1957, 1964, and 1969, and were studied again in summer, 1975. Two measurements, at 3-7 years following logging and post-logging treatment, and at 11-17 years afterward, are available for four stands; and three measurements at 7, 14, and 25 years after logging are available for one stand.

The purpose of this report is to describe trends in species composition and ground cover on these sites and factors influencing trends. Three sites occur in hemlock/ pachistima and two in grand fir/pachistima habitat types (Daubenmire and Daubenmire, 1968).

[1] A contribution of U.S. Forest Service, Intermountain Forest and Range Experiment Station, Intensive Timber Culture Project #44-364, University of Idaho, College of Forestry, Wildlife and Range Sciences, McIntire Stennis Project MS-22; and School of Forestry, University of Montana. Contribution no. 85, Forestry, Wildlife and Range Experiment Station, University of Idaho.

TABLE 1. Location, habitat type, and silvicultural treatment of stands examined in this study.

| Site | County | Legal location | Slope | Aspect | Elevation | Habitat type | Cut date | Slash disposal | Planted |
|---|---|---|---|---|---|---|---|---|---|
| Beetle Creek | Shoshone | T.51N, R.3E, S 15 | 45% | 150 | 1,150 m | Hemlock/pachistima | 1956 | Burn 1958 | 1961 White pine Douglas-fir |
| Jupiter Creek-Diamond Cut | Shoshone | T.51N, R.4E, S 31 | 35% | 210 | 1,045 m | Hemlock/pachistima | 1950 | No burn | None |
| Jupiter Creek-Power Line | Shoshone | T.51N, R.4E, S 31 | 35% | 210 | 1,045 m | Hemlock/pachistima | 1961 | Burn 1961 | None |
| Tourist Creek | Shoshone | T.51N, R.3E, S 2 | 45% | 135 | 1,075 m | Grand fir/pachistima | 1964 | Burn Sept. 1964 | 1965 Douglas-fir Grand fir |
| Mullan Tree | Kootenai | T.49N, R.1W, S 6 | 50% | 170 | 1,085 m | Grand fir/pachistima | 1961 | Burn Aug. 1961 | 1962 Douglas-fir Grand fir |

## Methods and Study Areas

Sites selected for study constituted potential big game winter range, were at low elevations near the main river, and were southerly exposed. A sequence of line-point intercepts was used to sample woody vegetation on all sites. On Beetle Creek, Jupiter Creek-Power Line, Jupiter Creek-Diamond Cut, and Tourist Creek sites, a 33-m steel tape was stretched 1 m above the ground. Any part of vegetation intercepting a vertical plane 0-2.3 m high at 0.3-m intervals along the tape was recorded. A rod was used to locate the vertical plane. Vegetation on the Mullan Tree site was too dense to follow this procedure in 1975, so a compass bearing was established and intercept of vegetation at 0.3-m intervals along this bearing was determined.

Intercept of each species of woody vegetation at each point was recorded. Understory vegetation, conifer seedlings on the site, and adjacent mature timber were inspected to determine habitat type following Daubenmire and Daubenmire (1968). Percent botanical composition was computed as:

$$\frac{\text{Number of intercepts for one species}}{\text{Number of intercepts for all species}} \times 100.$$

Percent ground cover for each species was calculated as:

$$\frac{\text{Total number of intercepts on species}}{\text{Total possible intercepts}} \times 100.$$

Percent ground cover for each species was summed to obtain total ground cover. Overlapping canopies contributed to values exceeding 100 percent in five cases. Scientific plant names follow Hitchcock and Cronquist (1973).

Three different statistical tests were used to determine significant changes for species on each site. The null hypothesis was that no change in vegetation cover occurred over the intervals measured. A chi-square test of independence was calculated at 0.05 level for those five species having the highest cover values in 1975 on each site. If a significant difference was determined, a Bonferoni Z statistic (Neu *et al.*, 1974) was used to determine the interval of the proportion of occurrence. A Wilcoxon sign test was used to determine significant changes in ground cover values for all plant species through time on each site (Huntsberger and Billingsley, 1973).

## Results

*Botanical composition of tall and low shrub unions:* The tall shrub union comprised species generally over one meter tall, including *Acer glabrum, Amelanchier alnifolia, Ceanothus sanguineus, C. velutinus, Cornus stolonifera, Holodiscus discolor, Philadelphus lewisii, Physocarpus malvaceus, Prunus emarginata, Prunus virginiana, Rhamnus purshiana, Salix scouleriana, Sambucus racemosa,* and *Sorbus scopulina.* The low shrub unions, less than one meter tall, were comprised of *Berberis repens, Lonicera utahensis, Pachistima myrsinites, Ribes* spp., *Rosa gymnocarpa, Rubus parviflorus, Spiraea betulifolia, Symphoricarpos albus,* and *Vaccinium membranaceum.* Tree species were considered separately.

Species representative of the low shrub union which were common to more mature stands increased in percent of total botanical composition in the four logged and burned stands during the study period (Fig. 1). Rate of increase was more rapid on hemlock/

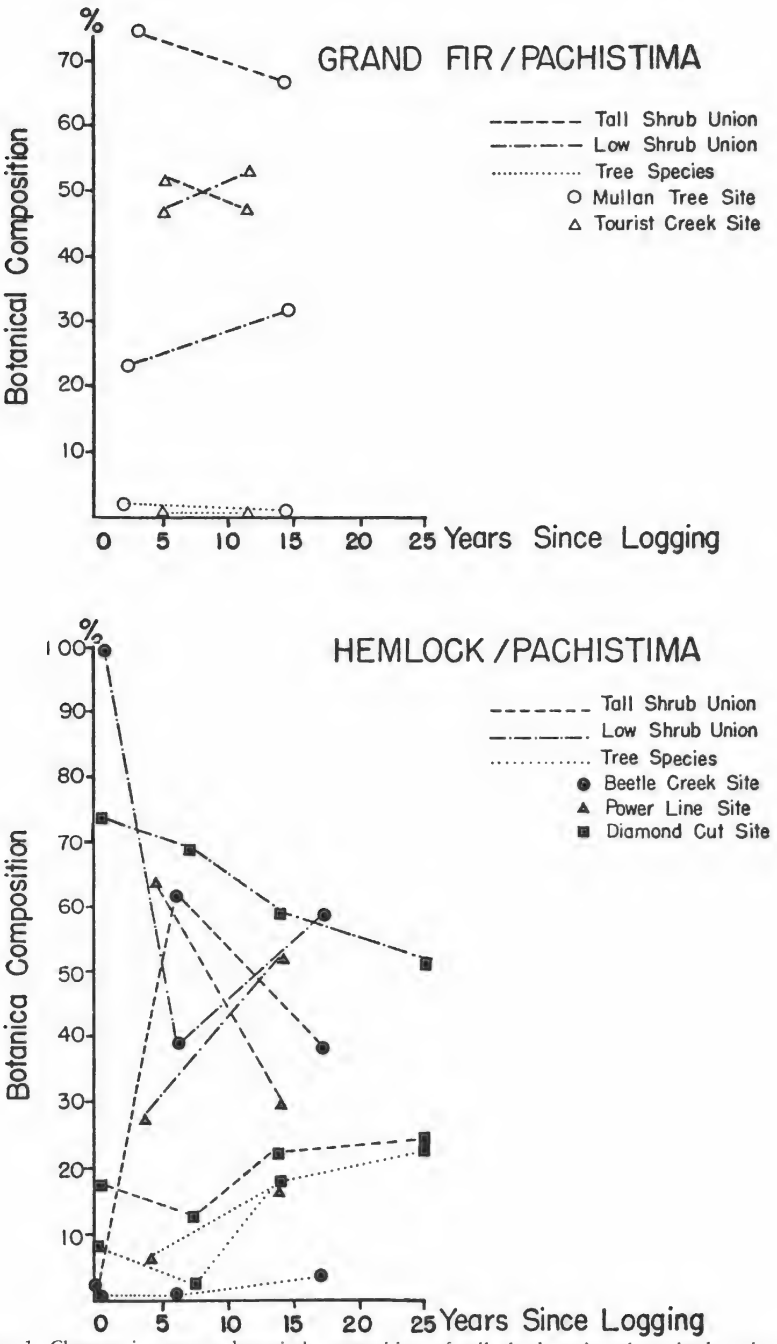


Figure 1. Changes in percent botanical composition of tall shrub union, low shrub union, and tree species on two grand fir/pachistima and three hemlock/pachistima sites following logging.

pachistima sites than on grand fir/pachistima sites. The site not burned after cutting, Diamond Cut, was the only site on which the low shrub union decreased in composition over an 18-year period.

Tall shrubs, dominant on all burned sites 3-7 years after logging, all decreased in percent composition at 11-17 years (Fig. 1). The rate of decrease was more rapid on hemlock/pachistima sites than on grand fir/pachistima sites. Tall shrubs dominated only one burned grand fir/pachistima site (Mullan Tree) in 1975, 14 years after logging. Tall and low shrubs essentially codominated the other three burned sites. The tall shrub union was still increasing in percent ground cover on the unburned hemlock/pachistima site, but percent botanical composition of tall shrub union was decreasing on this burned site after 14 years.

*Unlogged sites:* Two unlogged areas on hemlock/pachistima adjacent to logged sites at Diamond Cut and Beetle Creek were examined in 1957 (Table 2 and 6). Three low shrub species, *Pachistima myrsinites, Rosa gymnocarpa,* and *Vaccinium membranaceum,* comprised 99 percent of the shrub composition on the Beetle Creek site, while five species, *Abies grandis, Pachistima myrsinites, Rosa gymnocarpa, Symphoricarpos albus,* and *Vaccinium membranaceum,* were important on the Diamond Cut site. *Amelanchier alnifolia, Berberis repens, Rosa gymnocarpa, Spiraea betulifolia,* and *Symphoricarpos*

TABLE 2. Botanical composition and ground cover on the Jupiter Creek-Diamond Cut site prior to logging and 7, 14, and 25 years after logging. A * indicates significant difference using chi-square and Bonferoni Z test at 0.05 level. M indicates species was included in miscellaneous categories by Pengelly (1966). T indicates trace, or less than 0.1%. Change in species cover values significant using Wilcoxon test at 0.05 level.

| # of intercepts | 430 | | 496 | | 300 | | 300 | |
|---|---|---|---|---|---|---|---|---|
| | Unlogged adjacent | | 1957 (7-yr) | | 1964 (14-yr) | | 1975 (25-yr) | |
| Species | Comp. % | Cover % | Comp. % | Cover % | Comp. % | Cover % | Comp. % | Cover % |
| *Abies grandis* | 8.7 | 3.7 | 2.9 | 1.6 | 10.2 | 7.3 | 20.1 | 29.3* |
| *Acer glabrum* | M | M | M | M | 5.1 | 3.7 | 0.7 | 1.0 |
| *Amelanchier alnifolia* | 4.2 | 2.1 | 8.3 | 5.4 | 5.6 | 4.0 | 5.7 | 8.3 |
| *Berberis repens* | 8.7 | 3.7 | 19.3 | 14.1 | 2.8 | 2.0 | 1.6 | 2.3 |
| *Ceanothus sanguineus* | — | — | T | T | — | — | 0.2 | 0.3 |
| *Ceanothus velutinus* | — | — | — | — | 10.2 | 7.3 | 12.2 | 18.0* |
| *Cornus stolonifera* | — | — | M | M | 0.9 | 0.7 | — | — |
| *Holodiscus discolor* | 2.1 | — | 1.4 | — | — | — | 0.5 | 0.7 |
| *Lonicera utahensis* | — | — | — | — | — | — | 0.7 | 1.0 |
| *Pachistima myrsinites* | 8.7 | 3.5 | 1.4 | 0.6 | 3.7 | 2.7 | 12.1 | 17.7* |
| *Physocarpus malvaceus* | — | — | — | — | — | — | 0.5 | 0.7 |
| *Populus trichocarpa* | M | M | M | M | — | — | 0.5 | 0.7 |
| *Prunus* spp. | — | — | — | — | — | — | 1.6 | 2.3 |
| *Pseudotsuga menziesii* | M | M | M | M | — | — | 1.4 | 2.0 |
| *Ribes* spp. | M | M | M | M | 0.5 | 0.3 | — | — |
| *Rosa gymnocarpa* | 21.6 | 9.5 | 8.3 | 5.9 | 6.5 | 4.7 | 4.1 | 6.0 |
| *Rubus parviflorus* | M | 1.4 | M | 8.7 | 15.8 | 11.3 | 10.8 | 16.0 |
| *Salix scouleriana* | M | M | M | M | — | — | 3.4 | 5.0 |
| *Sambucus racemosa* | — | — | T | T | — | — | — | — |
| *Sorbus scopulina* | — | — | M | M | 0.5 | 0.3 | — | — |
| *Spiraea betulifolia* | 2.1 | 1.2 | 13.9 | 9.5 | 1.4 | 1.0 | — | — |
| *Symphoricarpos albus* | 8.7 | 3.7 | 19.3 | 13.7 | 20.0 | 14.3 | 15.0 | 22.7 |
| *Tsuga heterophylla* | M | 6.1 | — | — | 7.9 | 5.7 | 1.6 | 2.3 |
| *Vaccinium membranaceum* | 19.8 | 8.8 | 7.0 | 4.6 | 8.8 | 6.3 | 6.8 | 10.0 |
| Misc. bot. comp. | 15.4 | | 18.2 | | — | | — | |
| Total cover | | 43.7 | | 64.1 | | 71.6 | | 146.3 |

*albus* were more abundant in these stands than in stands cited by Daubenmire and Daubenmire (1968), being somewhat more comparable to old-growth stands of this habitat type described by Pfister *et al.* (1974). These stands illustrate some of the understory variation expected in western hemlock stands on southerly exposed sites in this region.

*Logged and unburned site:* The Diamond Cut site was not burned following cutting in 1950 (Table 2). Total ground cover of shrubs increased significantly from unlogged to 25 years post-logging. Five trends were apparent among the 12 species which accounted for 5 percent or more of botanical composition at one interval or more over the 25-year period. *Ceanothus velutinus* was not recorded in the unlogged stand or at 7 years following logging, but was third most prominent species at 25 years. *Abies grandis* and *Pachistima myrsinites* decreased initially at 7 years following logging, but then increased to higher values at 25 years than in unlogged adjacent stands. *Rosa gymnocarpa, Tsuga heterophylla,* and *Vaccinium membranaceum* appeared to decrease through the period. *Salix scouleriana* was increasing toward the later stages also, and may become more important at later stages. *Amelanchier alnifolia* showed no real change over the 25-year period. *Acer glabrum, Berberis repens, Rubus parviflorus, Spiraea betulifolia,* and *Symphoricarpos albus* increased initially after logging, but were decreasing at 25 years, the decrease occurring later for *Acer glabrum* and *Symphoricarpos albus* than for the other species.

*Logged and burned sites:* Four sites were clearcut and burned, two in grand fir/pachistima and two in hemlock/pachistima (Table 1). The two grand fir/pachistima sites differed in post-logging response. *Pachistima myrsinites* was absent from the Tourist Creek site (Table 3), with *Physocarpus malvaceus* constituting a major portion of

TABLE 3. Botanical composition and ground cover on the Tourist Creek site 5 and 11 years after logging. A * indicates significant difference using chi-square and Bonferoni Z test at 0.05 level. Change in species cover values not significant using Wilcoxon test at 0.05 level.

| # of intercepts | 300 1969 (5-yr) | | 300 1975 (11-yr) | |
|---|---|---|---|---|
| Species | Comp. % | Cover % | Comp % | Cover % |
| *Acer glabrum* | 0.5 | 0.3 | 1.9 | 1.7 |
| *Amelanchier alnifolia* | 6.5 | 4.7 | 1.5 | 1.3 |
| *Berberis repens* | 8.3 | 6.0 | 4.7 | 4.0 |
| *Ceanothus sanguineus* | 14.3 | 10.3 | 14.0 | 12.3 |
| *Ceanothus velutinus* | 0.5 | 0.3 | 4.7 | 4.0 |
| *Holodiscus discolor* | 10.1 | 7.3 | 1.9 | 1.7 |
| *Lonicera utahensis* | 0.9 | 0.7 | 6.1 | 5.3* |
| *Physocarpus malvaceus* | 15.7 | 11.3 | 17.8 | 15.7 |
| *Prunus* spp. | 2.3 | 1.7 | 4.7 | 4.0 |
| *Pseudotsuga menziesii* | — | — | 0.3 | 0.3 |
| *Rosa gymnocarpa* | 0.9 | 0.7 | 3.8 | 3.3 |
| *Rubus parviflorus* | 0.5 | 0.3 | — | — |
| *Sambucus racemosa* | — | — | 0.8 | 0.7 |
| *Sorbus scopulina* | 2.3 | 1.7 | — | — |
| *Spiraea betulifolia* | 3.7 | 2.7 | 6.8 | 6.0 |
| *Symphoricarpos albus* | 33.5 | 24.3 | 30.7 | 27.0 |
| *Vaccinium membranaceum* | — | — | 0.3 | 0.3 |
| Total cover | | 72.3 | | 87.6 |

the composition at 5 and 11 years after logging. Total shrub ground cover on this site did not change significantly over the six-year period between measurements, with the only significant change in composition being an increase in *Lonicera utahensis*. *Symphoricarpos albus* was the dominant species on this site. Six species accounted for 88 percent of the composition in 1969 and 80 percent in 1975.

*Ceanothus sanguineus* dominated the other grand fir/pachistima site, Mullan Tree (Table 4). Significant increases in *C. sanguineus, Pachistima myrsinites, Salix scouleriana,* and *Symphoricarpos albus* occurred from 3 to 14 years after logging. Total shrub ground cover increased to 174 percent at 14 years, with most of this attributable to the increase in *C. sanguineus*. Percent botanical composition of *C. sanguineus* decreased through this period. This decrease correlated with increases in all other species except *Rosa gymnocarpa.*

The two logged and burned sites in hemlock/pachistima showed similar trends in species composition (Tables 5 and 6). *Pachistima myrsinites* was abundant in the uncut adjacent stand, decreased initially, and then became the dominant or second-most dominant shrub at 14-17 years after logging. *Rosa gymnocarpa* was prominent in the uncut stand, but progressively decreased following logging. *Vaccinium membranaceum* decreased following logging, but may have reversed this trend in the Beetle Creek site at 17 years following cutting. *Ceanothus velutinus* was absent in the uncut stand, increased rapidly at 3-6 years following logging, and decreased thereafter. *Abies grandis, Berberis repens, Populus trichocarpa, Rubus parviflorus, Salix scouleriana, Spiraea betuli-*

TABLE 4. Botanical composition and ground cover on the Mullan Tree site 3 and 14 years after logging. A * indicates significant difference using chi-square and Bonferoni Z test at 0.05 level. Change in species cover values significant using Wilcoxon test at 0.05 level.

| # of intercepts | 2,000 1964 (3-yr) | | 1,978 1975 (14-yr) | |
|---|---|---|---|---|
| Species | Comp. % | Cover % | Comp % | Cover % |
| *Abies grandis* | — | — | 0.1 | 0.2 |
| *Acer glabrum* | 1.2 | 0.6 | 1.6 | 2.9 |
| *Alnus* spp. | — | — | 1.2 | 2.0 |
| *Amelanchier alnifolia* | — | — | 0.3 | 0.4 |
| *Berberis repens* | 1.0 | 0.5 | 2.6 | 4.6 |
| *Betula papyrifera* | 1.2 | 0.6 | — | — |
| *Ceanothus sanguineus* | 63.9 | 35.4 | 41.4 | 72.1 |
| *Holodiscus discolor* | — | — | 1.6 | 2.8 |
| *Larix occidentalis* | 0.1 | 0.1 | 0.1 | 0.2 |
| *Lonicera utahensis* | — | — | 0.1 | 0.2 |
| *Pachistima myrsinites* | 1.3 | 0.7 | 5.6 | 9.8* |
| *Philadelphus lewisii* | — | — | 0.4 | 0.8 |
| *Physocarpus malvaceus* | 1.7 | 1.0 | 2.2 | 3.8 |
| *Prunus* spp. | 0.3 | 0.2 | 1.3 | 2.3 |
| *Pseudotsuga menziesii* | 0.5 | 0.3 | 1.1 | 1.9 |
| *Ribes* spp. | 2.3 | 1.3 | 0.3 | 0.5 |
| *Rosa gymnocarpa* | 10.7 | 5.9 | 3.7 | 6.4 |
| *Rubus parviflorus* | 1.2 | 0.6 | 3.2 | 5.6 |
| *Salix scouleriana* | 7.3 | 4.0 | 16.6 | 29.0* |
| *Sambucus racemosa* | 0.2 | 0.1 | 0.1 | 0.2 |
| *Spiraea betulifolia* | 1.5 | 0.9 | 1.6 | 2.7 |
| *Symphoricarpos albus* | 5.5 | 3.0 | 14.8 | 25.6* |
| *Thuja plicata* | — | — | T | 0.1 |
| Total cover | | 55.2 | | 174.2 |

*folia,* and *Symphoricarpos albus* all sustained increases following logging, through the 17-year period. *Ceanothus sanguineus* was not abundant on either site, as contrasted to the high presence on grand fir sites. Total shrub ground cover increased dramatically over the 17-year period on both sites.

*Trends in shrub composition:* The tall shrub union in logged and burned stands on the hemlock/pachistima sites appeared to reach its peak in botanical composition at 3-5 years following logging (Fig. 2). This growth rate coincided with the rapid development of *Ceanothus velutinus.* Opposite trends occurred for the low shrub union and for many other species in the tall shrub union. As tree species gain dominance, both low and tall shrub unions would be expected to decrease rapidly, with the less shade-tolerant taller shrubs decreasing at a more rapid rate. If this trend is linear, the tall shrub union may drop below 10 percent of botanical composition between 25 and 30 years following cutting and burning.

Development of the tall shrub union in the unburned stand on hemlock/pachistima sites will probably not reach the levels on the burned sites, and appears to be delayed, reaching a peak at 20-25 years following cutting (Fig. 2). The trends appear to be primarily dependent upon the appearance and rate of growth of *Ceanothus velutinus,* which developed much earlier on the burned sites than on the unburned site. Tree species appeared to be reaching dominant status in the unburned site more rapidly than on the burned sites. As trees gain dominance, the low shrub union should decrease

TABLE 5. Botanical composition and ground cover on the Jupiter Creek-Power Line site 3 and 14 years after logging. A * indicates significant difference using chi-square and Bonferoni Z test at 0.05 level. Change in species cover values significant using Wilcoxon test at 0.05 level.

| # of intercepts | 700 | | 624 | |
|---|---|---|---|---|
| | 1964 (3-yr) | | 1975 (14-yr) | |
| Species | Comp. % | Cover % | Comp % | Cover % |
| *Abies grandis* | 3.0 | 2.0 | 7.1 | 13.8 |
| *Amelanchier alnifolia* | 0.2 | 0.1 | 1.3 | 2.4 |
| *Berberis repens* | 1.3 | 0.9 | 0.9 | 1.8 |
| *Ceanothus sanguineus* | — | — | 1.3 | 2.4 |
| *Ceanothus velutinus* | 62.9 | 41.4 | 20.0 | 38.8 |
| *Holodiscus discolor* | — | — | 1.3 | 2.7 |
| *Lonicera utahensis* | — | — | 0.5 | 1.0 |
| *Pachistima myrsinites* | 5.9 | 3.9 | 24.4 | 47.6* |
| *Pinus contorta* | — | — | 0.8 | 1.4 |
| *Populus tremuloides* | — | — | 0.3 | 0.5 |
| *Populus trichocarpa* | 3.5 | 2.3 | 7.4 | 14.3* |
| *Prunus* spp. | — | — | 1.6 | 3.0 |
| *Pseudotsuga menziesii* | 0.2 | 0.1 | 0.7 | 1.3 |
| *Rhamnus purshiana* | — | — | 0.3 | 0.5 |
| *Ribes* spp. | 5.2 | 3.4 | 4.7 | 9.0 |
| *Rosa gymnocarpa* | 0.4 | 0.3 | 0.8 | 1.6 |
| *Rubus parviflorus* | 7.6 | 5.0 | 12.2 | 23.7* |
| *Salix scouleriana* | 1.7 | 1.1 | 5.0 | 9.6 |
| *Sambucus racemosa* | 0.7 | 0.4 | 0.1 | 0.2 |
| *Spiraea betulifolia* | — | — | 0.8 | 1.6 |
| *Symphoricarpos albus* | 5.4 | 3.6 | 7.1 | 13.6* |
| *Tsuga heterophylla* | — | — | 0.6 | 1.1 |
| *Vaccinium membranaceum* | 2.0 | 1.3 | 0.8 | 1.4 |
| Total cover | | 65.8 | | 193.3 |

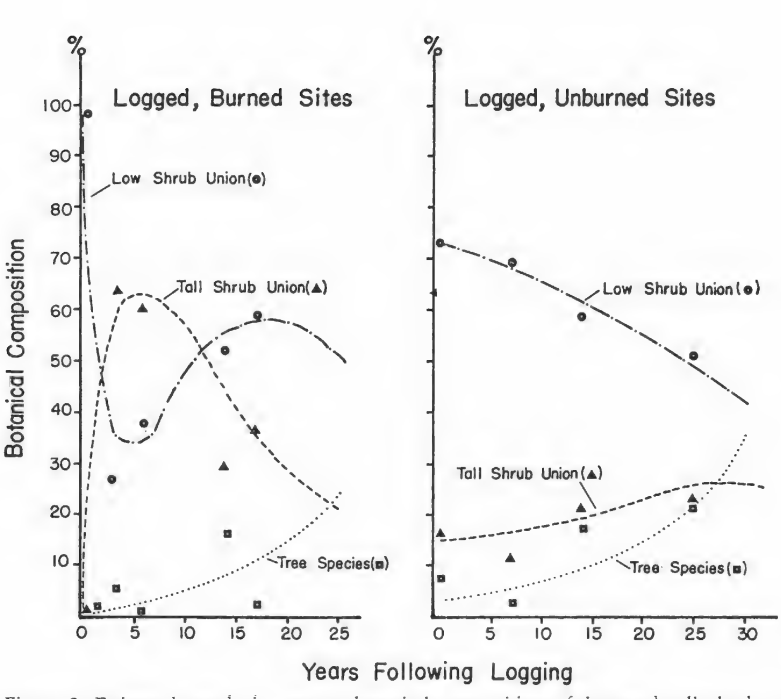


Figure 2. Estimated trends in percent botanical composition of low and tall shrub unions and tree species following logging on hemlock/pachistima habitat types.

TABLE 6. Botanical composition and ground cover on the Beetle Creek site prior to logging and 6 and 17 years after logging. A * indicates significant difference using chi-square and Bonferoni Z test at 0.05 level. M indicates species was included in miscellaneous categories by Pengelly (1966). T indicates trace, or less than 0.1%. Change in species cover values significant using Wilcoxon test at 0.05 level.

| # of intercepts | 418 Unlogged adjacent | | 1,000 1964 (6-yr) | | 999 1975 (17-yr) | |
|---|---|---|---|---|---|---|
| Species | Comp % | Cover % | Comp. % | Cover % | Comp. % | Cover % |
| *Abies grandis* | T | T | — | — | 0.3 | 0.6 |
| *Acer glabrum* | M | M | 1.1 | 1.1 | 0.8 | 1.4 |
| *Amelanchier alnifolia* | T | T | 1.3 | 1.3 | 1.4 | 2.5 |
| *Berberis repens* | T | T | 2.2 | 2.2 | 4.5 | 7.8 |
| *Ceanothus sanguineus* | — | — | — | — | 0.1 | 0.1 |
| *Ceanothus velutinus* | — | — | 58.3 | 59.5 | 33.6 | 58.7 |
| *Holodiscus discolor* | T | T | 0.4 | 0.4 | 1.4 | 2.4 |
| *Lonicera utahensis* | — | — | — | — | 1.2 | 2.5 |
| *Pachistima myrsinites* | 59.6 | 34.0 | 7.0 | 7.1 | 22.3 | 39.0* |
| *Populus trichocarpa* | — | — | — | — | 0.3 | 0.5 |
| *Prunus* spp. | M | M | 0.2 | 0.2 | 0.2 | 0.3 |
| *Pseudotsuga menziesii* | M | M | 0.1 | 0.1 | 2.5 | 4.4 |
| *Rosa gymnocarpa* | 14.0 | 8.0 | 7.5 | 7.6 | 0.6 | 1.1 |
| *Rubus parviflorus* | T | T | 5.5 | 5.6 | 5.0 | 8.8 |
| *Salix scouleriana* | M | M | 0.1 | 0.1 | 0.7 | 1.3 |
| *Sambucus racemosa* | M | M | 0.1 | 0.1 | 0.1 | 0.2 |
| *Spiraea betulifolia* | T | T | 9.7 | 9.9 | 13.3 | 23.2* |
| *Symphoricarpos albus* | T | T | 1.7 | 1.8 | 4.7 | 8.2 |
| *Vaccinium membranaceum* | 26.3 | 15.0 | 4.9 | 5.0 | 6.9 | 12.0 |
| Total cover | | 57.0 | | 102.0 | | 175.0 |

also, but less rapidly than the less shade-tolerant taller shrub species. As the stands mature and thin out, the low shrub union should again proliferate, as has been reported by Tappeiner (1971).

*Ceanothus sanguineus* determined tall shrub dominance and disappearance on the two grand fir/pachistima sites. It dominated the Mullan Tree site, and appeared to be decreasing at a more rapid rate than was the entire tall shrub union, while the low shrub union increased. Trends in these two sites were not as readily ascertainable as those on the hemlock sites, and dominance of tree species appeared to be delayed further than for hemlock/pachistima sites.

Maximum development of tall shrub unions in all burned sites in both habitat types appeared to be considerably earlier than that proposed by Lyon (1971) on much drier Douglas-fir sites in south-central Idaho, as would be expected. Development of the tall shrub union on the unburned hemlock/pachistima site was comparable, however.

#### Discussion

The quick regeneration of shrubs after fire reported by Cronemiller (1959) is well demonstrated here, with all sites having over 50 percent total cover values in less than seven years after treatment. After initial increases in shrub cover on all sites, a divergence appears with cover on three burned sites continuing to increase to very high values, while cover on one burned and one unburned site apparently stabilized at lower values.

No major invasion by the tall shrub union on the unburned site was noted, and beginning at 14 years after cutting, a substantial amount of ground was covered by conifers. At 25 years after cutting, 34 percent of the site was dominated by naturally established conifers.

*Symphoricarpos albus,* a low shrub, was dominant on the Tourist Creek site. A large proportion (two-thirds) of young conifers on the site were Douglas-fir; 88 percent of the timber cut from this site was Douglas-fir (Forest Service records 1956, 1964). Adjacent forest was a mixture of Douglas-fir and grand fir, with larger trees being 30-45 cm in diameter, and a sparse low shrub union. This site may be most xeric of the four burned sites, and may not have been as severely burned or as disturbed during logging as the other three sites.

The association of *Ceanothus* species with high shrub ground cover values was also documented by Mueggler (1965). Our data also support the view proposed by Dyrness (1973), Zavitkowski and Newton (1968), and Isaac (1940) that invader species dominate on burned sites. The early and continued dominance by one species on a site (Steen, 1966) is also supported. Further, most species which attained over 5 percent ground cover remained important in the stand over the study period.

Proposed trends on the logged and burned sites appear primarily related to rate of deterioration of *Ceanothus* species. A number of factors may accelerate this deterioration, including extreme cold coupled with lack of snow, insect attacks, and browsing by ungulates (Leege and Hickey, 1975), all of which were readily apparent on these sites. These factors would tend to decrease the period of dominance of *Ceanothus* species on these sites, and could hasten the inevitable dominance of tree species over proposed trends.

Conifers, especially grand fir, were established more rapidly on the unburned site. It is thus theorized that the unburned sites, with less *Ceanothus*, will succeed more

quickly to a mixture of conifers, of which grand fir will initially be important in both habitat types. The time span to mature western hemlock in hemlock/pachistima habitat type was apparently at least one successional sequence of conifers removed from that stage in which conifers initially dominated sites following logging.

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# Fungi in Streams, Lakes, Adjacent Soils, and Sewage Treatment Systems in the Flathead River Basin, Montana

## Abstract

In the study of fungal populations of waters, bottom sediments, and shore line samples of materials from streams, lakes, and sewage treatment plants in the Flathead River Basin and adjacent areas in western Montana, 89 species and other categories of fungi were recovered (Table 1). Larger amounts of observed or unnoticed organic matter were considered to be present where larger numbers of species or colonies of fungi were recovered.

## Introduction

During the summer session, June 24 through August 17, 1974, a class in Aquatic Microbiology at the University of Montana's Flathead Lake Biological Station studied samples of waters, bottom sediments, bank soils, and materials from sewage treatment plants which they collected throughout the basin of the Flathead River and adjacent territory. Although Potter and Baker (1956, 1961a and b) had studied the microbiology of Flathead and Rogers Lakes, this was probably the first time most of these habitat-types had been sampled for fungi in this region. The purpose of the study was to demonstrate the presence or absence of such organisms in such habitats in a sparsely settled region which in places appeared to be relatively free of human involvement.

## Techniques

Techniques used were essentially those described by Cooke (1963), modified to fit the available facilities and the time limits imposed by the nature of class schedules. Samples were collected in the field, returned to the laboratory, and processed. Grab samples were obtained in glass vials whose mouths were snap-capped. In the case of streams and lake shores, samples of water were obtained at arm's length from the shore; similarly, samples of water and sediment were obtained in the stream bottom or lake bottom at arm's length from the shore. Bank soil samples were secured at or near the interface of the water and the shore. In other cases, samples were taken as opportunity permitted. In the laboratory, of these samples 15 ml were added to 135 ml water to start the dilution series, and pairs of 15 ml portions of the samples were evaporated at 99° or 101°C to determine the dry weight of the sample from which the numbers of colonies per gram weight could be calculated. Flasks containing 1:10 dilution samples were placed on a 14-place shaker and shaken gently for half an hour, during which time the plating medium was prepared. Stream and lake waters were plated at 1:10, sewage and bottom sediments at 1:100 and 1:1000, and sludges and soils at 1:1000 and 1:10,000. To obtain dilutions of samples higher than 1:10, after shaking 5 ml of the 1:10 dilution were added to 45 ml water, 5 ml of this 1:100 dilution were added to another 45 ml of water, and 5 ml of this 1:1000 dilution were added to 45 ml water for the 1:10,000 dilution. For dispersion, each of these flasks was shaken by hand for a short period of time before materials were withdrawn for additional dilutions or plating. Since all platings were first-time events, the pairs of dilutions were used

to determine which would be better to use for the sample, or type of sample, being considered. Agar prepared for plating included neopeptone-dextrose-rose bengal agar, and neopeptone-dextrose agar. Each sample at dilutions of 1:10 and 1:100 were plated in triplicate, while duplicate plates were used for 1:1000 and 1:10,000 dilutions. Plating all dilutions in replicates of five would have been preferable, but supplies of Petri dishes were limited. Plates were labeled, the agar cooled to harden, and the plates were incubated right side up on the laboratory bench for one week. Room conditions of light and temperature prevailed; the plates were not kept in direct sunlight. At the end of a week the plates were inventoried, counted, and some colonies were observed directly with the microscope after spores were picked and placed in stock culture slants, using neopeptone-dextrose agar, for later study.

A second major technique involved the use of a liquid nutrient in shaken flasks. Two solutions were prepared, one of 2X strength Yeast-Nitrogen Base (YNB) (Difco), and one of 2 percent dextrose. These were filter sterilized separately. To each of as many sterile, cotton-stoppered flasks as there were samples collected were added 25 ml of each solution, giving a final medium of YNB-1 percent dextrose. One ml of the 1:10 dilution of each sample was added to each labeled flask. The flasks were shaken for a minimum of 64 hours. Three, four, or five days may be used, but after 72 hours most organisms will have appeared. When removed from the shaker, the flasks were tilted after several hours of settling, and a loopful of cells was removed from the meniscus between the liquid and the sediment on the bottom of the flask. This substance was streaked on the surface of a plate of yeast extract-malt extract-neopeptone-dextrose agar. Such plates were prepared in triplicate, labeled, and incubated on the laboratory bench for two or three days. Pure cultures were obtained by restreaking on the same type of agar as often as necessary, picking material to be streaked from as discrete colonies as possible. Most of the yeasts reported in Table 2 were obtained in this way. Insufficient time was available to complete the series of tests required for identification of many of the colonies obtained.

#### Sampled Locations

The sampled locations may be arranged in five groups:

*Lake shores with no obvious pollution at time of sampling:* Flathead Lake at the Biological Station, at the area used as a bathing beach, and at a point below the new dormitory near the point at which effluent from the Station's sewage treatment plant is discharged into the lake at some distance from the shore, near the Elwood Laboratory at the lake shore boat ramp, and in the boat dock area where a scum of pollen and other debris accumulated; Flathead Lake at a picnic area near Bigfork; Seeley Lake near the head of the lake behind the Flathead National Forest Ranger Station, at the Big Larch Campground boat ramp, on a sandy beach at the River Point Recreation Area, and at the Pine Glen Resort, a private campground and boat ramp; and Inez Lake at the boat ramp.

*Sewage Treatment System:* Polson sewage lagoons; Kalispell sewage treatment plant (STP), a primary type; Bigfork STP, a secondary-type with covered trickling filter; Biological Station STP, a tertiary-type with activated sludge; Glacier National Park, Lake MacDonald area STP, a secondary-type with a trickling filter; Missoula STP effluent in Clark Fork, a primary-type sewage treatment plant; and Columbia Falls STP, a secondary-type plant.

*Streams above and below points of discharge of sewage treatment plant effluents:* A stream entering Flathead Lake at Lakeside, sampled at Highway US-93, about a mile below the effluent of a lagoon treating sewage from a small military base, and at a point a few hundred feet below that effluent where a country road crosses the stream; Snyder Creek, Glacier National Park, above and below the point at which it received effluent from the Lake MacDonald area STP. It should be noted that above this sewage treatment plant, the stream serves an area along the Sperry Trail used as a comfort stop by horse-riding parties and hikers; the relatively unsightly toilets had been removed sometime before. South Fork of the Flathead River at the US-2 highway bridge; Clark Fork near Missoula a few hundred feet above the point at which effluent from the Missoula STP was discharged into it, but below a meat preparation plant, and other industries; and the North Fork of the Flathead River above and below the point of discharge of the effluent from the Columbia Falls STP.

*Apparently clean streams:* A clear stream draining woodlands at the Biological Station just above its confluence with Yellow Bay, and in Yellow Bay before mixing appeared to be complete; a clear stream crossing Montana SR-209, 1.5 miles north of Lion Creek, sampled upstream about 100 yd from the highway; a spring, in a rather dense thicket, tributary to Pauline Creek in the National Bison Range; and the Flathead River at Montana SR-207 just above Flathead Lake.

*Logan Pass:* Snow, bare soil, and sediments in a rill carrying snowmelt water, and soil under litter and duff under subalpine firs *(Abies lasiocarpa)*, below the Logan Pass Visitor Center parking lot, Glacier National Park.

## Results

In the study of 98 samples, a total of 89 species and other categories of fungi was obtained. The "other categories" include unidentified species in several genera, families, and other categories of fungi. These are listed, together with the localities in which the samples were obtained, in Table 2. Early in the study it was found that quantification of colonies would be relatively inconclusive because of the small number of replicate plates used, and the fact that most locations were sampled only once. Likewise, pH taken with pH paper strips was relatively unsatisfactory. However, the total *observation number* (ON) for each species is reported in Table 2. This value was obtained by adding together the numbers of times a species was observed on all plates studied, as well as the number of times identifiable colonies of yeasts were recovered from shaker flasks. The total number of fungus colonies observed was 6138.

## Discussion

Fungi are non-chlorophyllous, eukaryotic, heterotrophic organisms which cannot manu-

TABLE 1. Summary of species and observation numbers of fungi in five habitat groups in the Flathead River Basin.

| Habitat Group | Species | Percent of total (89) | Observation Number | Percent of total (6138) |
|---|---|---|---|---|
| 1 | 34 | 38.2 | 1749 | 28.3 |
| 2 | 35 | 39.3 | 1706 | 27.8 |
| 3 | 37 | 42.0 | 1738 | 28.3 |
| 4 | 14 | 15.7 | 251 | 4.1 |
| 5 | 13 | 14.6 | 371 | 6.0 |

TABLE 2. Species of fungi isolated from the Flathead Lake Basin, Observation Numbers, and locations from which species were recovered.

*Acremonium alternatum* Link ex S. F. Gray, Nat. Arr. Brit. Pl. 1: 550. 1821. ON-131.

Bank soil at Yellow Bay, Flathead Lake; water near head of Seeley Lake; scum on surface of Inez Lake at the boat ramp; sediment in creek one mile above Lakeside; influent to Kalispell STP*; settled sewage, Bigfork STP; influent to Biological Station STP; water, and bank soil, South Fork of Flathead River at US-2 bridge; water, and bank soil, Clark Fork above Missoula STP; water from Flathead Lake below new Biological Station dormitory; liquor in middle of aerator, and effluent from, Columbia Falls STP; bottom sediments, and bank soil, North Fork of Flathead River, above, and below, the Columbia Falls STP; sediment in and bank soil beside, rill carrying snowmelt water below Visitor Center, Logan Pass, Glacier National Park.

*Acremonium charticola* (Lindau) W. Gams, *Cephalosporium*-artige Schimmelpilze. 46. 1971.—ON-4.

Bottom sediments in Seeley Lake at Big Larch Campground boat ramp; and mud in swampy area adjacent to that boat ramp.

*Acremonium terricola* (Miller, Giddens & Foster) W. Gams, *Cephalosporium*-artige Schimmelpilze. 67. 1971.—ON-5.

Water near the head of Seeley Lake; mud in swampy area adjacent to boat ramp, Big Larch Campground, Seeley Lake; bottom sediments and bank soil, South Fork Flathead River at US-2 bridge.

*Acremonium vitellinum* W. Gams, *Cephalosporium*-artige Schimmelpilze. 65. 1971. ON-3.

Bottom sediments, Flathead River at Mont.-207; bottom sediments, Flathead Lake at a picnic area near Bigfork.

*Actinomucor elegans* (Eidam) C. R. Benjamin & Hesseltine, Mycologia 49: 241. 1957. ON-4.

Bank soil, shore of Yellow Bay at Biological Station boat ramp; and bank soil, North Fork Flathead River above effluent discharge point of the Columbia Falls STP.

*Alternaria alternate* (Fries) Keissler, Beih. Bot. Centr. 29: 434. 1912. ON-96.

Bottom sediments in Flathead Lake below the new dormitory at the Biological Station, first and sixth sampling period; water, and bank soil Flathead Lake shore used as bathing beach at Biological Station area; water, and bank soil, Yellow Bay at the Biological Station boat ramp; Yellow Bay water with scum at the Biological Station boat dock; Seeley Lake: water, and bottom sediments near the head of the lake, water at Big Larch Campground boat ramp; water at River Point beach; scum on Inez Lake at the boat ramp; water from a clear stream crossing Mont. 209 1.5 mi. north of Lion Creek; lagooned sewage at the Polson STP; water from a spring flowing into Pauline Creek, National Bison Range; water in a creek near Lakeside one mile above highway US-93; water, and sediment in that creek at the highway water, and bank soil on Flathead River at Mont.-207; raw sewage influent to Lake MacDonald STP, Glacier National Park; slime from trickling filter stones, Lake MacDonald STP; water, bottom sediment, and bank soil above effluent discharge point, and bottom sediment, and bank soil below effluent discharge point, Snyder Creek, Lake MacDonald STP, Glacier National Park; bank soil on Yellow Bay, Biological Station boat ramp area; water, and bank soil on Clark Fork above the Missoula STP; effluent, and upstream drift, from the Missoula STP; slime on rocks in that effluent stream; Talley Lake effluent collected by Dr. A. L. Sheldon and his class; liquor in middle of aerator, and effluent from, Columbia Falls STP; bank soil, North Fork Flathead River above Columbia Falls STP effluent discharge point; bottom sediment, and bank soil in rill carrying snowmelt water below the Logan Pass Visitor Center, and soil under *Abies lasiocarpa* above that rill, Glacier National Park.

*Alternaria tenuissima* (Kunze ex Persoon) Wiltshire, Tr. Brit. Myc. Soc. 18: 157. 1933. ON-1.

Bottom sediments, Seeley Lake at Big Larch Campground boat ramp.

*Aspergillus* sp. ON-15.

Water from Flathead River at Mont.-207.

*Aspergillus flavus* Link ex Link. Species plantarum 6: 66. 1824. ON-45.

Bank soil on Flathead Lake shore area used as bathing beach at the Biological Station; slime on stones on trickling filter at Lake MacDonald STP, Glacier National Park; bottom sediments, and bank soil on Clark Fork above the Missoula STP; influent to the Columbia Falls STP; bank soil on North Fork Flathead River above effluent outfall of the Columbia Falls STP; bank soil along a rill carrying snowmelt runoff, and soil under *Abies lasiocarpa* above that rill, below the Logan Pass Visitor Center, Glacier National Park.

*Aspergillus fumigatus* Fresenius, Beitr. Mykologie 81. 1863. ON-4.

Sediment in Flathead Lake below the new Biological Station dormitory; and water in Yellow Bay at the Biological Station boat ramp.

*Aspergillus niger* van Tieghem, Ann. Sci. Nat. Bot., Ser. 5. 8: 240. 1867. ON-7.

Effluent from Polson lagoons; water and bank soil on Flathead River at Mont.-207; water at Yellow Bay Biological Station boat ramp; and bank soil on North Fork Flathead River below effluent discharge point of Columbia Falls STP.

*Aspergillus ochraceus* Wilhelm, Inaugr. Diss., Strassbourg. 66. 1877. ON-1.

Bank soil on Clark Fork above the Missoula STP.

*Aspergillus sydowii* (Bainier & Sartory) Thom & Church, The Aspergilli 147. 1926. ON-3.

TABLE 2. (Continued)

Water from South Fork Flathead River at US-2 bridge; melting snowbank below the Logan Pass Visitor Center, Glacier National Park.

*Aureobasidium pullulans* (deBary) Arnaud, Ann. Sci. Agr., Montpelier, N.S. 16: 39. 1918. ON-11.

Raw sewage, and secondary settled sewage, Lake MacDonald STP, Glacier National Park; bank soil on Clark Fork above the Missoula STP.

*Beauvaria bassiana* (Balsano) Vuillemin, Bull. Soc. Bot. Fr. IV. 12: 40. 1912. ON-5.

Bank soil on Flathead Lake shore area used as bathing beach at the Biological Station; water from Seeley Lake, and mud from swampy area, at boat ramp, Big Larch Campground; final effluent of Kalispell STP after receiving massive dose of chlorine.

*Candida* spp. ON-31.

Sewage in activator at Biological Station STP; influent to plant, and liquor in middle of aerator, Columbia Falls STP.

*Candida curvata* (Diddens & Lodder) Lodder & Kreger-van Rij, The Yeasts. Ed. 1: 576. 1952. ON-10.

Effluent from Polson lagoons; and influent to Columbia Falls STP.

*Candida ?robusta* Diddens & Lodder, Die Anaskosporogenen Hefen. 2. 1942. ON-9.

Sewage in activator, Biological Station STP.

*Cephalosporium* sp. ON-5.

Water in a clear stream before its confluence with Yellow Bay.

*Cladosporium* sp. ON-21.

Water, and bank soil at Biological Station boat ramp, Yellow Bay; water with scum at Yellow Bay boat dock; bank soil at the bathing beach, Flathead Lake Biological Station; water in a clear stream above its confluence with Yellow Bay; scum on water at boat ramp on Inez Lake; bottom sediments in creek crossing US-93 at Lakeside, and at a country road crossing a mile above Lakeside; water from Flathead Lake at a picnic area near Bigfork.

*Cladosporium cladosporioides* (Fresenius) de Vries, Contrib. *Cladosporium* 57. 1952. ON-495.

Isolated from 65 of the 98 samples taken, including clean as well as apparently polluted samples.

*Cladosporium elatum* (Harz) Nannfeldt, Svenska Skogsvårdsför. Tidsk. 1934: 422. ON-4.

Water from Seeley Lake at the Pine Glen Resort; effluent from lagoon 2 in lagoon 1, in the Polson STP; and effluent from the Polson STP.

*Cladosporium ?epiphyllum* Persoon, sensu Gilman, Man. Soil Fungi ed. 2: 334. 1957. ON-2.

Flathead Lake water from below the new Biological Station dormitory; sediment in Seeley Lake near the Big Larch Campground boat ramp.

*Cladosporium herbarum* S. F. Gray, Nat. Arr. Brit. Pl. 1: 556. 1821. ON-36.

Flathead Lake water, and bottom sediments, from below the new Biological Station dormitory; water from Yellow Bay at the Biological Station boat ramp; water in Seeley Lake at the Big Larch Campground boat ramp; water from lagoon 2 in lagoon 1, and effluent from the Polson STP; water from a spring along Pauline Creek in the National Bison Range; bank soil on Snyder Creek below the Lake MacDonald STP effluent; and sediment in rill carrying snowmelt water below Logan Pass Visitor Center, Glacier National Park.

*Cladosporium sphaerospermum* Penzig, Michelia 2: 473. 1882. ON-6.

Water from Yellow Bay at the Biological Station boat ramp; water from a clear stream entering Yellow Bay at the Biological Station; water in Clark Fork in upstream drift of Missoula STP effluent.

*Colletotrichum coccodes* (Wallroth) Hughes, Can. J. Bot. 36: 754. 1958. ON-1.

Primary settled sludge, Lake MacDonald area STP, Glacier National Park.

*Colletotrichum gloeosporioides* Penzig, Fungi Agron. 2: 6. 1882. ON-2.

Water from Seeley Lake at the Pine Glen resort; bank soil on Snyder Creek below the Lake MacDonald STP outfall, Glacier National Park.

*Curvularia lunata* (Wakker) Boedijn, Bull. Jard. Bot. Buitenzorg, III. 13: 127. 1933. ON-6.

Bottom sediments, Yellow Bay at the Biological Station boat ramp; water from the South Fork Flathead River at the US-2 bridge; water from Clark Fork below the Missoula STP effluent discharge point.

*Epicoccum purpurrascens* Ehrenberg ex Schlechtendahl, Flora Berol. 2 (crypt.): 136. 1824. ON-4.

Bank soil from Flathead Lake below the new Biological Station dormitory; scum on water at the Inez Lake boat ramp; water in a creek near Lakeside, a mile above US-93; sewage in the Kalispell STP at the comminutor with preliminary chlorination.

*Emericellopsis donezkii* Beljakova. Mikol. Fitopatol. 8(5): 387. 1974. ON-1.

Lakeshore sediment, Wayfarer's Wayside, Flathead Lake, Bigfork.

*Fusarium* spp. ON-53.

Water in Yellow Bay at the Biological Station boat ramp; bank soil near the head of Seeley Lake; bank soil on Seeley Lake at the Big Larch Campground boat ramp; scum on water of Inez Lake at the boat ramp; bottom sediments from the South Fork Flathead River at the US-2 bridge; and influent to the Columbia Falls STP.

*Fusarium oxysporum* Schlechtendahl, Flora Berol. 2: 139. 1824. emend. Snyder & Hansen, Am. J. Bot. 27: 64-67. 1940. ON-23.

Bank soil on Yellow Bay at the Biological Station boat ramp; water in Yellow Bay at the con-

TABLE 2. (Continued)

fluence of a clear creek; scum on water of Inez Lake at the boat ramp; primary settled sewage sprayed on covered trickling filter at the Bigfork STP; secondary settled sewage, and primary settled sludge, Lake MacDonald STP, Glacier National Park; and bank soil on Clark Fork above the Missolua STP.

*Fusarium roseum* Link ex Fries complex. ON-43.

Bank soil on Flathead Lake below the new Biological Station dormitory; water, and bottom sediments in Flathead Lake area used for a bathing beach at the Biological Station; bank soil on Seeley Lake at the Big Larch Campground boat ramp; bottom sediments in stream a mile above US-93 at Lakeside; and primary settled sewage sprayed on the covered trickling filter at Bigfork STP.

*Geotrichum candidum* Link ex Persoon, Myc. Eur. 1: 26. 1822. ON-186.

Bank soil on a creek one mile above US-93 at Lakeside; bottom sediments in Flathead Lake at a picnic site near Bigfork; sewage in activator at the Biological Station STP—abundant; raw sewage entering Lake MacDonald STP—abundant; bottom sediment in Snyder Creek downstream from effluent outfall of Lake MacDonald STP. Glacier National Park.

*Gliocladium catenulatum* Gilman & Abbott, Iowa St. Col. Jour. Sci. 1: 303. 1927. ON-1.

Bank soil near the head of Seeley Lake.

*Gliocladium fimbriatum* Gilman & Abbott, Iowa St. Col. Jour. Sci. 1: 304. 1927. ON-2.

Bank soil near the head of Seeley Lake.

*Gliomastix murorum* (Corda) Hughes var. *felina* (Marchal) Hughes, Canad. J. Bot. 36: 769. 1958. ON-1.

Bank soil on Clark Fork above the Missolua STP.

*Humicola grisea* Traaen, Nyt. Mag. Naturved. 52: 34. 1914. ON-2.

Water in Yellow Bay below the confluence of a clear creek.

*Leptosphaeria* sp. ON-1.

Water in Yellow Bay below the confluence of a clear creek.

*Monilia acremonium* Delacroix sensu Gilman, Man. Soil Fungi, ed 2: 208. 1957. ON-8.

Bottom sediments in a clear stream above its confluence with Yellow Bay; sediments in Yellow Bay below that confluence; chlorinated final product of Biological Station STP.

*Mucor* sp. ON-9.

Bottom sediments in Flathead River at Mont.-207; primary settled sludge at Lake MacDonald STP; water in Snyder Creek above outfall of Lake MacDonald STP, Glacier National Park; bank soil in North Fork Flathead River below outfall of Columbia Falls STP.

*Mucor hiemalis* Wehmer, Ann. Mycol. 1: 39. 1903. ON-387.

Water, and bank soil, on Yellow Bay at the Biological Station boat ramp; scum on water of Inez Lake at boat ramp; bank soil on Flathead Lake at picnic area near Bigfork; raw sewage influent to Lake MacDonald STP; primary and secondary settled sewage, and slime on trickling filter stones in the Lake MacDonald STP—abundant; water, and bottom sediments in Snyder Creek above and below the outfall of the Lake MacDonald STP, Glacier National Park; bottom sediments and bank soil on South Fork Flathead River at US-2 bridge; bank soil on North Fork Flathead River above outfall of Columbia Falls STP; bottom sediments, and bank soil on North Fork Flathead River below outfall of Columbia Falls STP.

*Mucor janssenii* Lendner, Muc. d. l. Suisse 88. 1908. ON-39.

Bank soil on Snyder Creek above the outfall of the Lake MacDonald STP, Glacier National Park; bottom sediment, and bank soil on the South Fork Flathead River at US-2 bridge; water and sediment on Clark Fork above the Missoula STP; effluent of the Missoula STP; water in Clark Fork carrying effluent drift upstream; slime on rocks in Missolua STP effluent stream; bank soil on Flathead Lake below the new Biological Station dormitory; water and bank soil on Yellow Bay at the Biological Station boat ramp; sewage in middle of aerator, and effluent, Columbia Falls STP.

*Mucor plumbeus* Bonorden, Abt. Naturf. Ges. Halle 8: 109. 1864. ON-4.

Water from Yellow Bay at Biological Station boat ramp; bottom sediment in creek a mile above Lakeside; raw sewage influent to Lake MacDonald STP, Glacier National Park; bank soil on South Fork Flathead River at US-2 bridge.

*Myrothecium roridum* Tode ex Fries, Syst. Myc. 3: 217. 1829. ON-1.

Bank soil on Seeley Lake at Big Larch Campground boat ramp.

*Paecilomyces marquandii* (Mason) Hughes, CMI Mycol. Papers 45: 30. 1951. ON-2.

Water in a clear stream above its confluence with Yellow Bay; primary settled sewage at the Lake MacDonald STP, Glacier National Park.

*Paecilomyces varioti* Bainier, Bull. Soc. Myc. Fr. 23: 26-27. 1907. ON-6.

Bottom sediments in Yellow Bay below the confluence of a clear stream; bank soil on Snyder Creek above effluent of Lake MacDonald STP, Glacier National Park.

*Penicillium* spp. ON-695.

Isolated from 59 of 98 sampled stations, sometimes abundantly.

*Penicillium fellutanum* Biourge, Monogr., La Cellule 33(1): 262-264. 1923. ON-3.

Water in Yellow Bay just below confluence of a clear stream; slime on stones in a covered trickling filter, Bigfork STP; sediment in Flathead Lake just below the new Biological Station dormitory.

TABLE 2. (Continued)

*Penicillium frequentens* Westling, Arkiv für Botanik II: 58, 133-134. 1911. ON-1.
Sediment in South Fork Flathead River at US-2 bridge.

*Penicillium funiculosum* Thom, USDA Bur. Anim. Ind. Bull. 118: 69. 1910. ON-3.
Effluent from the lagoons in the Polson STP; bank soil on Clark Fork above the Missoula STP; bank soil along rill carrying snowmelt water below the Logan Pass Visitor Center, Glacier National Park.

*Penicillum humuli* van Beyma, Zentbl. f. Bakt., etc. II. 99: 392-394. 1939. ON-2.
Bank soil at the Yellow Bay Biological Station boat ramp.

*Penicillium ochro-chloron* Biourge, Monogr., La Cellule 33(1): 269-270. 1923. ON-42.
Stream bottom sediments, and bank soil on Clark Fork above the Missoula STP.

*Penicillium piscarium* Westling, Arkiv für Botanik 11: 54, 86-88. 1911. ON-2.
Water from a spring draining into Pauline Creek, National Bison Range.

*Penicillium purpureogenum* Stoll, Beitr. z. Morph. u. Biol. char. *Penicillium,* Wurzburg. 32. 1904. ON-1.
Stream bottom sediments, Clark Fork above the Missoula STP.

*Penicillium variabile* Sopp, Monogr. 169-171. 1812. ON-10.
Water, and bank soil on Clark Fork above the Missoula STP; bank soil on the North Fork Flathead River, above the Columbia Falls STP.

*Pestalotia* sp. ON-5.
Most species of *Pestalotia* are presently identified on the basis of the vascular plant which is host to them. Few species are satisfactorily identified from other habitats at present.
Water from Flathead Lake below the new Biological Station dormitory; bottom sediments in a clear stream above its confluence with Yellow Bay; water, and bottom sediments in Yellow Bay below confluence with a clear stream; water in Seeley Lake at the Big Larch Campground boat ramp.

*Phoma* spp. ON-180.
Isolates assigned here have several types of pycnidia, but without knowing the nature of the potential plant hosts, the reaction in culture of various types of such pathogens, or the method of spore production, assignment to exact genus and species is impractical at present.
Isolated from 26 of 98 samples, sometimes abundantly.

*Phoma eupyrena* Saccardo, Michelia 1(5): 525. 1879. ON-5.
Bank soil, bathing beach area, Flathead Lake, Biological Station; water, and sediments, Seeley Lake, at Big Larch Campground motor boat ramp; effluent from lagoon 1, and at Polson sewage lagoons.

*Phoma herbarum* Westendorp sensu Gilman, Man. Soil Fungi Ed. 2: 198. 1957. ON-2.
Water in Yellow Bay at the Biological Station boat ramp; and water near the head of Seeley Lake.

*Phoma putaminum* Spegazzini. Atti Soc. Critogam. Ital. 1; 66. 1881. ON-1.
Scum on water surface, Inez Lake at motor boat ramp.

*Phoma radicis-callunae* Rayner, Bot. Gaz. 73: 231. 1922. ON-3.
Primary settled liquor, Bigfork STP; influent, and secondary settled sewage, Lake MacDonald area STP, Glacier National Park.

*Pyrenochaeta terrestris* (Hansen) Gorens, Walker & Larsen, Phytopath. 38: 838. 1948. ON-1.
Bank soil from the shore of Flathead Lake below the new Biological Station dormitory.

*Rhinocladiella mansonii* (Castellani) Schol-Schwarz, Antoni van Leeuwenhoek 34: 122-133. 1968. ON-13.
Bottom sediment at the Yellow Bay Biological Station boat ramp; bank soil near the head of Seeley Lake; influent raw sewage to the Kalispell STP; water, and bottom sediments in Flathead Lake at a picnic area near Bigfork; primary settled sewage in the Bigfork STP; water in Clark Fork above the Missoula STP; water in Flathead Lake below the new Biological Station dormitory; liquor in the middle of the aerator at the Columbia Falls STP.

*Rhizopus nigricans* Ehrenberg, Nova Acta Acad. Leop. 10(1): 198. (1818) 1820. ON-4.
Bottom sediments in Flathead Lake below the new Biological Station dormitory; bottom sediments in Clark Fork above the Missoula STP; effluent from the Columbia Falls STP; bank soils on the North Fork Flathead River, above and below the effluent stream from the Columbia Falls STP.

*Rhodotorula* spp. ON-529.
Isolated from 21 of the 98 samples tested, sometimes abundantly. Highest numbers of observations were made in bottom sediments, and bank soils, in Flathead Lake below the new Biological Station dormitory. At this point the effluent from the Biological Station STP is discharged into the lake at a little distance from the shore.

*Stachybotrys chartarum* (Ehrenberg ex Link) Hughes, Canad. J. Bot. 36: 812. 1958. ON-1.
Raw sewage influent to the Columbia Falls STP.

*Stagonospora samarorum* (Desmazières) Boerema. Persoonia 6:25. 1970. ON-1.
Wet marshy soil near motor boat ramp, Big Larch Campground, Seeley Lake.

*Streptomyces* sp. ON-273.
Colonies of *Streptomyces* species rarely appear on media such as used in these recovery attempts.

TABLE 2. (Continued)

However, on solid media 19 samples yielded occasional or abundant colonies of at least one species assignable to this genus of fungus-like prokaryotic organisms.

Water, and bank soil on Yellow Bay at the Biological Station boat ramp; sediments in Yellow Bay below the confluence of a clear stream; bank soil on Seeley Lake at the Big Larch Campground boat ramp; water, and bank soil from Clark Fork above the Missoula STP; bottom sediments, and bank soil from the South Fork Flathead River at the US-2 bridge; effluent from the Missoula STP, and from upstream drift of this effluent in Clark Fork; water from Flathead Lake below the new Biological Station dormitory; bank soil on the North Fork Flathead River above the outfall of the Columbia Falls STP; bottom sediments, and bank soil below that outfall; a melting snowbank, sediment, and bank soil on a rill carrying snowmelt water, and soil under *Abies lasiocarpa,* below the Logan Pass Visitor Center, Glacier National Park.

*Tilachlidium brachiatum* (Batsch ex Fries) Petch in E, A, Ellis, Trans. Norfolk Norwich. Nat. Soc. 15: 198. 1940. ON-74.

Bottom sediments and bank soil on Clark Fork above the Missoula STP; upstream drift of Missoula STP effluent in Clark Fork; bottom sediments in Yellow Bay at the Biological Station boat ramp; bank soil on the North Fork Flathead River above the outfall of the Columbia Falls STP.

*Torulopsis* sp. ON-8.

Effluent of the lagoons of the Polson STP.

*Trichoderma longibrachiatum* Rifai, CMI Mycol. Papers 116: 42. 1969. ON-3.

Bottom sediments and bank soil at a picnic area on Flathead Lake near Bigfork.

*Trichoderma viride* Person ex S. F. Gray, Nat. Arr. Brit. Pl. 1: 560. 1821. *sensu latissimo.* ON-82.

Isolated from 22 of the 98 samples tested, sometimes abundantly.

*Trichosporon* spp. ON-37.

Bank soil near head of Seeley Lake; bank soil on Seeley Lake at Big Larch Campground boat ramp; primary settled liquor at Bigfork STP; final product of Biological Station STP; raw sewage and primary settled sewage at the Lake MacDonald STP; water, and bank soil on Snyder Creek below the Lake MacDonald STP, Glacier National Park; effluent from Talley Lake collected by Dr. Sheldon and his class.

*Trichosporon cutaneum* (de Buerrmann, Gougerot & Vaucher) Ota, Ann. Parasitol. Hum. Comp. 4: 1. 1926. ON-11.

Effluent from the Missoula STP, upstream drift from that effluent and downstream water after mixing, in Clark Fork; liquor in the middle of the aerator, Columbia Falls STP; bottom sediment and bank soil in North Fork Flathead River above the discharge point of the Columbia Falls STP.

*Trichosporon cutaneum* var. *multisporum* (Cochet) Lodder & Kreger-van Rij, The Yeasts, Ed. 1: 625. 1952. ON-45.

While this variety is a habitat variant no longer accepted as a taxonomic entity, its occurrence in these habitats may be of interest.

Bank soil near the head of Seeley Lake; sediment in creek at US-93 at Lakeside; raw sewage influent to the Kalispell STP; water from Clark Fork above the Missoula STP; slime on rocks in effluent stream from the Missoula STP; sediment in Yellow Bay at the Biological Station boat ramp.

*Ulocladium* sp. ON-3.

Water from Flathead Lake shore area used as bathing beach at the Biological Station; bank soil, Flathead Lake, Biological Station.

*Ulocladium atrum* Preuss, Linnaea 25: 75. 1852. ON-7.

Water in Yellow Bay below confluence of a clear stream; sediment on sandy beach on Seeley Lake at River Point picnic area; bank soil on stream one mile above Lakeside; bank soil on Snyder Creek below outfall of Lake MacDonald STP, Glacier National Park; bank soil on Clark Fork above Missoula STP; effluent from Columbia Falls STP; sediment in rill carrying snowmelt water below Logan Pass Visitor Center, Glacier National Park.

*Ulocladium consortiale* (von Thuemen) Simmons, Mycologia 59: 84. 1967. ON-16.

Water and bank soil, at Yellow Bay Biological Station boat ramp; water in a clear stream 100 yd above Mont.-209 1.5 miles n. of Lion Creek; lagooned sewage flowing from pond 1 to pond 2, Polson STP; water from a spring flowing into Pauline Creek, National Bison Range; sediment in a stream at US-93 at Lakeside; effluent from Missoula STP drifting upstream in Clark Fork; bank soil in North Fork Flathead River below effluent of Columbia Falls STP; sediment in rill carrying snowmelt water, and soil under *Abies lasiocarpa* above that rill, below Logan Pass Visitor Center, Glacier National Park.

*Verticillium chlamydosporum* Goddard, Bot. Gaz. 56: 275. 1913. ON-1.

Bank soil on Clark Fork above Missoula STP.

In addition, a number of unidentified colonies were recovered or observed:

Moniliaceae: From 81 of 98 samples. ON-777.

Damatiaceae: From 55 of 98 samples. ON-402.

White yeasts (in contrast with red yeasts, species of *Rhodotorula*): From 47 samples. ON-474.

*STP—Sewage treatment plant.

Note: "above" refers to "upstream from," or "uphill from"; "below" refers to "downstream from," or "downhill from."

facture their own food supplies. They are dependent on other organisms for preformed organic matter which may or may not then be reduced to elements, ions, carbon dioxide, and water from which the original organic matter was produced by green plants, or rearranged by consumer organisms. Fungi are thus reducer organisms. They secrete enzymes into the environment of a food substance available to be consumed, possibly polluting the environment to a certain extent; but they use the products of enzymatic action as nutrients which are further acted upon by endoenzymes once the cell wall and various internal membranes are passed through. Bacteria have similar processes, and since their cells are smaller, they have greater surface area. In spite of this fact, the fungi, with their more versatile enzyme systems, are more efficient reducer organisms than the bacteria; Isaac and James (1965) indicated that metabolic rates of bacteria are 33 cal/kg/hr; of fungi, 50-250 cal/kg/hr; and of protozoa, 1 cal/kg/hr. Unfortunately, beyond those bacteria involved in public health problems, little is known about bacteria in aquatic environments. Not a great deal more is known about those fungi which inhabit this environment. However, as the organic load increases, there appears to be a larger number of fungi, or of fungus colonies. Such colonies may be produced by larger numbers of species, or in some heavily polluted habitats there may be a reduction in number of species but an increase in numbers of colonies of those fungi adaptable to the particular situation.

Of the 89 species or species groups recovered, 43 were found fewer than 10 times for a total ON of 160. The remaining species were tabulated considering the five habitat-types described above (Table 1). It is interesting to note that Groups 1, 2, and 3, have similar observation numbers and numbers of species, while Groups 4 and 5 have similar and much lower observation numbers and fewer species. A more critical analysis of Groups 1, 2, and 3 should be based on such types of data as dissolved oxygen, total carbon, and other parameters used in describing the pollution characteristics of streams and waters. Obviously, increased amounts of organic matter are present in these three types of stations, regardless of the appearance of any habitat sampled. This fact is quite apparent in some cases, less so in others.

Of the 43 more common species, none are restricted to habitat groups 4 and 5. Of species found only in one or another sample in habitat groups 1, 2, and 3, all have been found in a variety of studies elsewhere. The implication here is that in processing only one sample per location, the total population was not recovered. Even the survey of two or three plates per dilution per sample probably did not yield a complete list of the species present since the effect of the law of diminishing returns is not usually evident until five to eight plates have been poured from a dilution of one sample. Three species of yeasts were recovered only from samples from habitat group 2. These three yeasts have been recovered from other habitats and cannot be considered *lymabionts,* organisms restricted to a heavily polluted habitat. All of the 46 species represented by more than 9 observation numbers are probably *lymaphiles*, species of organisms which adapt easily to conditions of increased organic loads. Of the remaining 43 species, most may be considered *lymaxenes,* species which can tolerate conditions of increased organic matter in the habitat. Species represented by only one or two observation numbers may be considered lymaxenes rather than *lymaphobes,* species which cannot tolerate pollution loads, on the basis of other studies of similar habitats. Within the limits of this study, lymaphobes would be difficult to pinpoint.

Should one try to characterize the stations by their populations of fungi recovered in this study in relation to possible increases in organic matter, the shore of Flathead Lake below the new Biological Station dormitory near the point at which treated sewage is dumped into the lake is indicated as the most polluted of the natural waters sampled. There is no experimental information concerning the effect of chlorine on fungi disseminules; colonies on the primary isolation plates may have originated from pieces of mycelium as well as spores. This fact is evident from the populations of fungi recovered from effluent streams of the Kalispell and the Biological Station sewage treatment plants, both of which were reported to be chlorinated. Clean water, water not available for contamination by man's activities, such as the spring near Pauline Creek in the National Bison Range, yielded few fungal colonies, and between these extremes fungi were present to greater or lesser extents. One of the more interesting areas studied was Seeley Lake. This lake is a kidney-shaped body of water with the outlet on one side instead of at the apparently lower end. Resorts and communities at the lower end of the lake find themselves in a situation where currents bring water, and whatever may be added to it, to the lower end. Whatever is carried in that water tends to pile up rather than be carried around to River Point where the outlet carries water from Seeley Lake to the Blackfoot River, a tributary of Clark Fork. Thus, while not draining into the lake directly, but through a septic tank system, a resort operation like that at Pine Glen Resort could be blamed for the results of discharges of its neighbors.

Many of the same organisms were present in two areas in the western states which had been studied in relation to pollution problems largely based on industrial wastes effluents. These areas included the Bear River in the Cache Valley of southeastern Idaho and northeastern Utah, and the Cache la Poudre River in Colorado (Cooke, 1967, 1968).

#### Conclusions

Fungi are present in good numbers in stream habitats and sewage treatment plants throughout the Flathead River Valley and in adjacent areas. They can be isolated from a variety of habitats ranging from spring water to raw sewage. Increased abundance indicates the presence of larger and larger amounts of organic matter which serves as their food supply. Sources of such organic matter include sewage treatment systems, treated, or usually untreated household and agricultural drainage, and natural leaf-fall.

#### Acknowledgments

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# Heavy Metals in Lakes of the Coeur d'Alene River Valley, Idaho[1]

**Abstract**

Heavy metal concentrations were measured in the water, sediments, and fish of nine small lakes located along the main stem of the Coeur d'Alene River. Mining wastes have been discharged into this drainage since the 1890s. Concentrations of dissolved metals were low in the water and did not differ significantly from lake to lake. Zn, Cu, Cd, and Pb have accumlated in lake sediments. The concentrations of these metals varied in sediments from lake to lake, and within each lake were highest at stations close to the river.

Zn, Cu, and Cd concentrations in muscle and liver of Yellow Perch were not significantly different among lakes. However, Zn and Cd concentrations in fish from several of the Coeur d'Alene lakes were significantly higher than in fish from a control area. Metal concentrations were somewhat related to trophic status, decreasing at higher trophic levels. Zn, Cu, and Cd concentrations were greater in benthic insects than in fish. The concentration of zinc in muscle was highest in Brown Bullheads (68 mg/kg), an omnivorous species, and lowest in Largemouth Bass (20 mg/kg), a piscivorous species.

## Introduction

Sewage and mining wastes have been discharged into the Coeur d'Alene River since the 1890s. Rock flour and heavy metals in the mining wastes have been deposited along the river and in the lake. Ellis (1932), in an extensive survey of this pollution problem, noted that the river was essentially devoid of life from the South Fork at Kellogg to the delta at Harrison, Idaho. He also noted that three of the lateral lakes along the river had sparse plankton and benthos populations, which he attributed to toxic effects of mine wastes.

In 1968-1969, settling ponds for mining and milling waste waters were installed. These measures reduced the suspended solids entering the river and decreased some of the dissolved elements, such as nickel and lead (Mink *et al.,* 1971). Dissolved zinc and cadmium, however, remained above toxic limits for most aquatic organisms.

The present study was undertaken to obtain more detailed information on occurrence of heavy metals in the water and sediments of the lateral lakes along the lower section of the Coeur d'Alene River; and secondly, to study accumulation of heavy metals in fish and insects from this area.

## Area Description

The nine lakes in this study lie along the lower 22 miles of the Coeur d'Alene River (Fig. 1). They are situated in the flood plains, and connected to the river by channels. The lakes are shallow; the deepest is only nine meters. In spring the lakes are usually flooded because the water table rises above the adjacent valley floor (Mink *et al.,*

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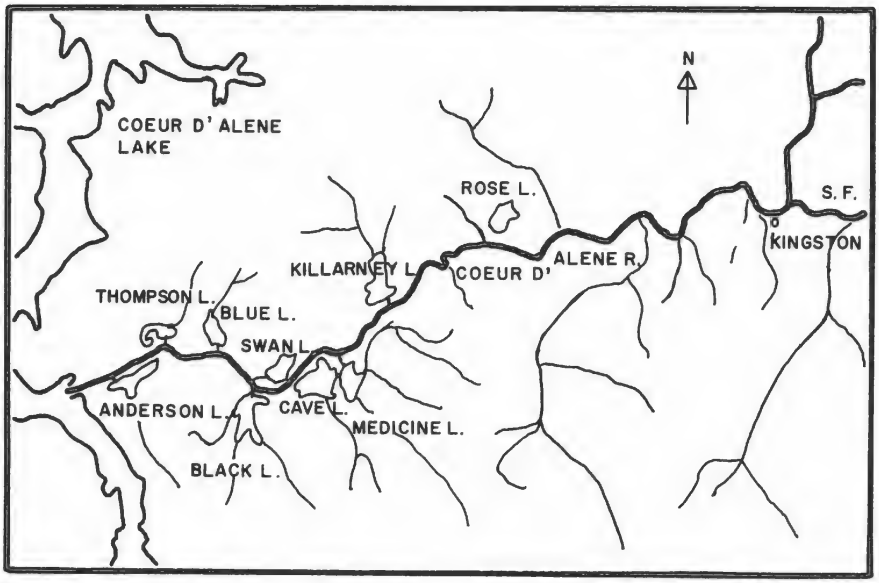


Figure 1. Main stem of the Coeur d'Alene River.

1971). The dam on the Spokane River, the outlet of Lake Coeur d'Alene, enhances this flooding process since it backs water up the river, and in turn raises the water level in the lakes. Later in the fall, as water is released from the dam, the water level is lowered in the main stem. The water level in turn drops in the lateral lakes as water flows back into the river.

Anderson, Black, Cave, and Medicine Lakes are located on the south side of Coeur d'Alene River and are separated from the river by a railroad levee (Figs. 1 and 2). Three of these lakes are connected to the river by long winding inlets. Cave Lake has no direct connection to the river during periods of low water. At flood stage, however, an open space in the railroad dike allows water to pass in and out. In addition, this lake is connected to Medicine Lake by a small channel.

Killarney, Rose, and Thompson Lakes are located on the north side of the river. Thompson Lake is separated from the river by a dike road and Rose Lake by a state highway. During highwater in spring, the river passes through a culvert and seeps across a marsh into Rose Lake. The inlet into Killarney Lake is a wide dredged out channel, approximately four meters deep.

Blue and Swan Lakes are also located on the north side of the river. No barrier separates these waters from the river. Both lakes were completely flooded in the spring of 1974 and could not be distinguished from the river.

Bell's Lake is located 17 mi upstream from Coeur d'Alene Lake. It was used as a control to represent background levels of metals in water, sediments, and fish. This lake is similar in size, depth, and chemical make-up to the lateral lakes off the Coeur d'Alene River, and is likewise flooded in high run-off years.

**Methods**

Water for heavy metal analysis was collected in acid-washed polyethylene bottles which

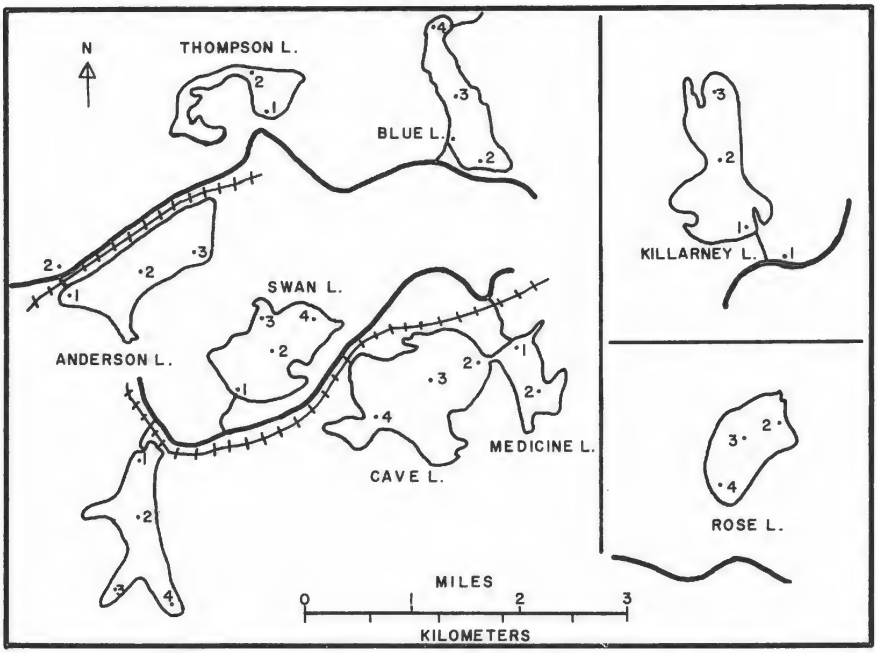


Figure 2. Stations in lakes of the Coeur d'Alene River valley.

were rinsed with lake water four to five times before sample was retained. These samples were kept frozen until analyzed. Dissolved oxygen and temperature were determined with a Model 51 Oxygen Meter (Yellow Springs Ins. Co.), pH with a Hellige pocket comparator, and specific conductance with a Solu Bridge conductivity meter. Alkalinity was measured by titration, and hardness by calculation according to Standard Methods (1972).

Bottom sediments were obtained with an Eckman dredge. The top 2-3 cm of sediment was scraped from the surface of the Eckman dredge load, and retained as a sample. This sample was placed in glass jars, and kept cool until analyzed.

The concentrations of metals were measured by a Perkin-Elmer model 303 Atomic Absorption Spectrophotometer (AAS). Detection limits for the metals considered are: zinc—0.05 mg/1; copper—0.02 mg/1; cadmium—0.02 mg/1; and lead—0.5 mg/1.

Water samples were aspirated directly into the spectrophotometer without prior treatment. Many investigators recommend acidification of water sample to a low pH level to prevent adsorption of metal ions to walls of the container (King *et al.,* 1974; Standard Methods, 1971). However, W. H. Funk (personal communication) advised that addition of acid might introduce error caused by leaching of metals from suspended solids. Water samples were frozen as an alternate method of preservation (Clement, 1972).

Fish muscle was obtained along and above the lateral line. Cross *et al.* (1973) found no significant differences in heavy metal concentrations in different sections of a fillet from a Bluefish, *Pomatomus saltatrix.* Therefore, location of the muscle sample probably has no effect on metal concentration.

Biological samples were wet-ashed for AAS analysis as modified from the methods of Thompson and Blanchflower (1971), as follows: Approximately one gram of desiccated tissue was digested in a mixture of 3 ml of distilled concentrated nitric acid and 1 ml of 70 percent perchloric acid (plus two glass beads) for about 2 hours, then evaporated to near dryness. Five ml of 5 percent $HNO_3$ were added to the ash, and 2.5 ml of this solution was used for cadmium analysis. The remaining original solution was diluted by an equal amount of 5 percent $HNO_3$ and was used for zinc and copper analysis. Two blanks were also set up with each run, and the average was subtracted from sample absorption before calculating the concentration in mg/kg dry weight.

Sediment samples were prepared for AAS analysis using the digestion procedures outlined in the Chemical Lab Manual for Bottom Sediments, Great Lake Region Committee (1969).

#### Results

*Water:* In 1973, the water in the lateral lakes was clear at the time of sampling, except near the inlets where it was turbid. This green-colored river water could be easily traced into Thompson Lake and Anderson Lake for about 100 meters. In 1974, the water in all the study lakes along the Coeur d'Alene River was turbid because of extremely high water that year.

The water was uniform in chemical composition and contained low levels of dissolved substances (Table 1). Specific conductance ranged from 55-92 micromhos, hardness from 14-22 mg/1 $CaCO_3$, and methyl orange alkalinity from 11-23 mg/1 $CaCO_3$. The pH was between 6.8 and 7.4. Dissolved oxygen at the surface was near saturation, and was never below 4 mg/1 at the bottom.

In the spring of 1973, cadmium, copper, and lead concentrations in the water were below AAS detection limits (see Methods); and zinc measurements varied within lakes. Dissolved zinc concentrations ranged from 0.34-0.44 mg/1 at the inlet stations in Swan Lake, Thompson Lake, and Anderson Lake. The range of concentrations is similar to the zinc concentration of 0.41 mg/1 in the river near these lakes. Values of 0.05-0.07 mg/1 zinc were recorded in the open water stations in these lakes. Similar concentrations of zinc occurred at the open water stations in Black Lake and Blue Lake, but zinc increased to 0.09 and 0.12 mg/1 respectively at the inlets. Zinc concentrations were as high as 1.1 mg/1 in the Coeur d'Alene River, but were below detection limits in Bell's Lake, which was used as a control.

The concentration of zinc at the open water stations of Killarney Lake was uniformly higher than the open water stations in other lakes. Zinc concentration at the inlet, however, was much lower than in the river. The wide inlet apparently transports a larger volume of river water into this lake and brings about a more thorough mixing than occurs in the other lakes.

In Rose Lake and Cave Lake zinc concentrations were below detection limits at all stations. These lakes have no direct connection to the river, but receive water from it indirectly at times of flooding in the spring.

Water chemistry data for 1974 were similar to those of 1973 (Table 2). The greater dilution caused by high spring run-off is apparently responsible for the decrease in conductivity and dissolved zinc.

*Sediments:* The concentrations of zinc, copper, cadmium, and lead in the sediments, as

TABLE 1. Chemical characteristics of the Coeur d'Alene River drainage, April-June 1973.

| Station* | | Temp (°C) | pH | D.O. (mg/1) | Cond. (μmhos) | M.O.Alk. (mg/1 $CaCO_3$) | Hardness (mg/1 $CaCO_3$) | Ca (mg/1) | Mg (mg/1) | Zn (mg/1) |
|---|---|---|---|---|---|---|---|---|---|---|
| Rose Lake | 2 | 22 | 7.0 | — | 80 | 14 | 15.6 | 3.3 | 1.8 | <0.05 |
| | 3 | 22 | 7.0 | — | 80 | 11 | 15.4 | 3.2 | 1.8 | <0.05 |
| | 4 | 22 | 7.0 | — | 80 | 14 | 15.6 | 3.3 | 1.8 | <0.05 |
| Killarney Lake | 1 | 20 | 7.0 | 7.0 | 80 | 16 | 20.6 | 4.6 | 2.2 | 0.24 |
| | 2 | 20 | 7.0 | 7.0 | 78 | 15 | 20.6 | 4.6 | 2.2 | 0.22 |
| | 3 | 20 | 7.0 | 6.5 | 78 | 17 | 20.6 | 4.6 | 2.2 | 0.22 |
| Medicine Lake | 1 | 12 | 7.0 | 8.0 | 55 | 15 | 12.8 | 2.8 | 1.4 | 0.05 |
| | 2 | 11 | 7.0 | 10.0 | 60 | 11 | 10.2 | 2.1 | 1.3 | 0.06 |
| | 3 | 12 | 7.0 | — | 60 | 12 | 9.6 | 1.9 | 1.2 | 0.06 |
| Cave Lake | 2 | 22 | 7.0 | 8.0 | 60 | 18 | 16.7 | 3.9 | 1.7 | <0.05 |
| | 3 | 22 | 7.0 | 7.0 | 60 | 15 | 16.7 | 3.9 | 1.7 | <0.05 |
| | 4 | 22 | 7.0 | 8.0 | 60 | 15 | 16.7 | 3.9 | 1.7 | <0.05 |
| Swan Lake | 1 | 14 | 7.0 | — | 80 | 17 | 18.5 | 3.6 | 2.2 | 0.44 |
| | 2 | 19 | 7.0 | — | 75 | 14 | 17.7 | 3.6 | 2.1 | 0.07 |
| | 3 | 19 | 7.0 | — | 75 | 14 | 17.7 | 3.6 | 2.1 | 0.07 |
| | 4 | 19 | 7.0 | — | 78 | 14 | 17.7 | 3.6 | 2.1 | 0.07 |
| Black Lake | 1 | 19 | 7.0 | 7.8 | 90 | 20 | 21.7 | 4.2 | 2.7 | 0.09 |
| | 2 | 19 | 7.0 | 7.8 | 90 | 22 | 21.6 | 4.2 | 2.7 | 0.04 |
| | 3 | 19 | 7.0 | 7.8 | 92 | 23 | 21.8 | 4.2 | 2.8 | 0.04 |
| | 4 | 19 | 7.0 | 7.8 | 90 | 21 | 22.2 | 4.2 | 2.9 | 0.04 |
| Blue Lake | 1 | 21 | 7.0 | 7.8 | 73 | 13 | 15.7 | 3.3 | 1.8 | 0.12 |
| | 2 | 21 | 7.0 | 7.3 | 70 | 14 | 14.2 | 2.9 | 1.7 | 0.06 |
| | 3 | 21 | 7.0 | 7.8 | 70 | 14 | 14.2 | 2.9 | 1.7 | 0.07 |
| | 4 | 21 | 7.0 | 7.8 | 72 | 14 | 14.3 | 2.9 | 1.7 | 0.06 |
| Thompson Lake | 1 | 14 | 7.0 | 6.0 | 60 | 15.5 | 14.5 | 2.9 | 1.7 | 0.41 |
| | 2 | 20 | 7.0 | 8.0 | 90 | 15 | 15.6 | 2.9 | 2.1 | 0.06 |
| Anderson Lake | 1 | 14 | 6.8 | 5.0 | 60 | 14.4 | 14.2 | 2.9 | 1.6 | 0.34 |
| | 3 | 20 | 7.0 | 8.0 | 80 | 14.4 | 17.6 | 3.7 | 2.4 | 0.05 |
| Coeur d'Alene River | 1 | 16 | 7.0 | 6.5 | 100 | 20 | 25.9 | 5.6 | 2.9 | 1.10 |
| | 2 | 14 | 7.0 | 6.5 | 60 | 14 | 14.4 | 2.9 | 1.6 | 0.41 |

*Station 1—inlet; stations 2 to 4—open water sites.

TABLE 2. Chemical characteristics of the Coeur d'Alene River drainage, June 1974.

| Station* | | Temp. (°C) | pH | Cond. (μmhos) | M.O. Akl. (mg/l $CaCO_3$) | Hardness (mg/l $CaCO_3$) | Ca (mg/l) | Mg (mg/l) | Zn (mg/l) |
|---|---|---|---|---|---|---|---|---|---|
| Rose Lake | 2 | 21 | 6.9 | 60 | 14 | 13.8 | 2.9 | 1.6 | <0.05 |
| | 3 | 20 | 6.9 | 65 | 12 | 14.0 | 3.0 | 1.6 | <0.05 |
| | 4 | 20 | 6.9 | 65 | 10 | 14.0 | 3.0 | 1.6 | <0.05 |
| Killarney Lake | 1 | 14 | 7.0 | 60 | 18 | 14.7 | 3.4 | 1.5 | 0.08 |
| | 2 | 17 | 7.0 | 60 | 18 | 11.4 | 3.4 | 1.4 | 0.08 |
| | 3 | 16 | 7.0 | 60 | 16 | 11.4 | 3.4 | 1.4 | 0.08 |
| Medicine Lake | 1 | 16 | 7.1 | <50 | 14 | 12.8 | 3.0 | 1.3 | <0.05 |
| | 2 | 19 | 7.2 | <50 | 14 | 13.6 | 3.3 | 1.3 | <0.05 |
| | 3 | 22 | 7.3 | <50 | 16 | 11.0 | 2.3 | 1.3 | <0.05 |
| Cave Lake | 2 | 20 | 7.2 | <50 | 14 | 12.6 | 2.8 | 1.3 | <0.05 |
| | 3 | 21 | 7.3 | <50 | 14 | 12.4 | 3.0 | 1.2 | <0.05 |
| | 4 | 23 | 7.4 | <50 | 12 | 12.0 | 3.0 | 1.1 | <0.05 |
| Swan Lake | 1 | 17 | 7.0 | 60 | 16 | 14.9 | 3.5 | 1.5 | 0.10 |
| | 2 | 17 | 7.0 | 60 | 18 | 14.8 | 3.3 | 1.6 | 0.10 |
| | 3 | 17 | 7.0 | 60 | 16 | 13.0 | 2.9 | 1.4 | 0.10 |
| | 4 | 16 | 7.0 | 60 | 18 | 14.8 | 3.3 | 1.6 | 0.10 |
| Black Lake | 1 | 22 | 7.3 | 80 | 18 | 19.6 | 4.4 | 2.1 | <0.05 |
| | 2 | 22 | 7.4 | 80 | 18 | 20.1 | 4.3 | 2.3 | <0.05 |
| | 3 | 23 | 7.3 | 90 | 18 | 24.0 | 5.5 | 2.5 | <0.05 |
| | 4 | 25 | 7.3 | 80 | 16 | 23.7 | 5.7 | 2.3 | <0.05 |
| Blue Lake | 1 | 16 | 7.0 | 60 | 16 | 14.5 | 3.5 | 1.4 | 0.11 |
| | 2 | 16 | 6.8 | 60 | 16 | 15.3 | 3.5 | 1.6 | 0.09 |
| | 3 | 18 | 7.0 | 60 | 16 | 15.3 | 3.5 | 1.6 | 0.08 |
| | 4 | 18 | 7.0 | 60 | 18 | 14.0 | 3.3 | 1.4 | 0.08 |
| Thompson Lake | 1 | 24 | 7.0 | 70 | 22 | 17.7 | 3.8 | 2.0 | <0.05 |
| | 2 | 24 | 7.0 | 70 | 20 | 14.9 | 4.0 | 1.2 | <0.05 |
| Anderson Lake | 1 | 23 | 7.0 | 65 | 18 | 14.6 | 3.2 | 1.6 | <0.05 |
| | 2 | 24 | 7.0 | 65 | 18 | 14.9 | 3.0 | 1.8 | <0.05 |
| | 3 | 24 | 7.0 | 65 | 18 | 14.5 | 3.0 | 1.7 | <0.05 |

*Station 1—inlet; stations 2 to 4—open water sites.

measured by Atomic Absorption, indicate a definite increase over background levels (Table 3). Zinc and lead concentrations were 10-40 times higher in the Coeur d'Alene lakes than in Bell's Lake sediments. Copper and cadmium concentrations were not elevated to the same extent, but show a definite increase over background. Bowen (1966) lists the world-wide averages for these metals in the soil as follows: copper-10, lead-10, zinc-50, and cadmium-0.06 mg/kg. Estimates of background levels in the Coeur d'Alene soil are similar to these world-wide averages (Channey, 1959).

Generally speaking, metal values were higher in sediments of lakes closer to the discharge of mining wastes. As a result, lakes that were more intimately connected to the river were higher in metal content. The highest concentrations occurred in Killarney Lake and the lowest in Rose Lake. The other Coeur d'Alene lakes were intermediate between these two. Swan Lake and Blue Lake were higher than lakes which were separated from the river by levees.

*Fish:* Observations of Yellow Perch, *Perca flavescens,* which were abundant in each lake, failed to show any consistently significant differences in metal content (Bauer, 1974). As a result, samples from all the lateral lakes were combined and compared with perch samples from the control lake (Table 4).

TABLE 3. Analysis of metals in sediments of the Coeur d'Alene River drainage as determined by AAS, Spring 1973.

| Station* | | Zinc (mg/kg) | Copper (mg/kg) | Cadmium (mg/kg) | Lead (mg/kg) | Iron (%) |
|---|---|---|---|---|---|---|
| Rose Lake | 2(1) | 240 | 21 | 2 | 100 | 0.5 |
| | 3(5) | 1900 | 23 | 14 | 2150 | 3.3 |
| | 4(5) | 2100 | 38 | 15 | 3200 | 3.9 |
| Killarney Lake | 1(4) | 4000 | 140 | 50 | 4600 | 9.3 |
| | 2(5) | 4250 | 160 | 55 | 3950 | 9.0 |
| | 3(2) | 5200 | 87 | 130 | 2550 | 4.6 |
| Medicine Lake | 1(1) | 2550 | 79 | 30 | 3000 | 8.7 |
| | 2(6) | 2950 | 87 | 44 | 2650 | 6.5 |
| Cave Lake | 2(3) | 2750 | 29 | 45 | 2300 | 2.2 |
| | 3(6) | 2800 | 60 | 34 | 2700 | 4.0 |
| | 4(8) | 3300 | 79 | 29 | 3850 | 5.5 |
| Swan Lake | 1(1) | 2600 | 112 | 25 | 3500 | 10.0 |
| | 2(6) | 2950 | 132 | 26 | 3850 | 9.3 |
| | 3(3) | 4650 | 138 | 57 | 3900 | 6.7 |
| | 4(2) | 1900 | 41 | 19 | 1800 | 7.0 |
| Black Lake | 1(1) | 2350 | 92 | 29 | 4700 | 8.5 |
| | 2(9) | 2600 | 38 | 29 | 1750 | 4.2 |
| | 3(5) | 2300 | 13 | 18 | 800 | 2.1 |
| | 4(2) | 1750 | 8 | 11 | 490 | 1.6 |
| Blue Lake | 1(1) | 2000 | 126 | 25 | 3400 | 9.2 |
| | 2(2) | 6800 | 112 | 83 | 3400 | 4.2 |
| | 3(8) | 3600 | 130 | 36 | 4200 | 6.1 |
| | 4(3) | 2750 | 27 | 38 | 950 | 2.3 |
| Thompson Lake | 1(1) | 3000 | 82 | 23 | 3700 | 9.3 |
| | 2(3) | 2900 | 52 | 31 | 2600 | 4.7 |
| Anderson Lake | 1(2) | 3250 | 76 | 46 | 2850 | 7.0 |
| | 2(5) | 3550 | 87 | 42 | 3350 | 4.1 |
| | 3(3) | 2150 | 34 | 56 | 1750 | 2.5 |
| Bell's Lake** | 2(4) | 110 | 4 | <2 | 30 | 2.2 |
| | 3(6) | 52 | 8 | <2 | <300 | 2.4 |
| | 4(3) | 100 | 9 | <2 | <300 | 2.0 |

*Station 1—inlet; stations 2 to 4—open water sites.
( ) = depth in meters.
**Bell's Lake—control, St. Joe River drainage.

TABLE 4. Mean metal concentration in Yellow Perch from Coeur d'Alene Lakes and control lake.[1]

| | Coeur d'Alene | | | Control Lake[2] | | | |
|---|---|---|---|---|---|---|---|
| | Mean (mg/kg) | ± 95% C.I. | N | Mean (mg/kg) | ± 95% C.I. | N | N-test |
| Zinc | | | | | | | |
| Muscle | 52.0 | 6.3 | 11 | 31.9 | 6.0 | 11 | 2.38** |
| Liver | 126.0 | 24.0 | 74 | 71.2 | 8.2 | 11 | 1.71* |
| Copper | | | | | | | |
| Muscle | 0.87 | 0.29 | 50 | 0.89 | 0.18 | 8 | N.S. |
| Liver | 16.5 | 7.3 | 32 | 12.9 | 2.4 | 8 | N.S. |
| Cadmium | | | | | | | |
| Muscle | 0.32 | 11.0 | 39 | 0.2 | — | 11 | — |
| Liver | 16.1 | 5.6 | 49 | 1.5 | — | 11 | — |

[1]Av. wt. of test fish was 40 g and control fish was 35 g.
[2]Bell's Lake in the St. Joe River drainage.
*0.10 probability level, **0.05 probability level.

The concentration of zinc was significantly higher in the perch from the Coeur d'Alene lakes than from Bell's Lake in the St. Joe drainage. Concentration of copper was somewhat similar to the fish from both areas. Although a statistical comparison cannot be made for cadmium since it was below detection limits in Bell's Lake, the metal was definitely elevated in the liver tissue of the fish from the test lakes.

Lucas *et al.* (1970) found 0.09 mg Cd/kg in white fish samples from the Great Lakes region, and 0.4 mg Cd/kg in liver tissue. Windom (1973) reported 0.2-1 mg/kg in muscle of marine fish and <0.1-5 mg/kg in the liver. In comparison, cadmium in the muscle of fish from the Coeur d'Alene lakes was similar (avg. .32 mg/kg), but concentrations in the liver tissues were much higher (avg. 16.1 mg/kg).

Metals in Yellow Perch from the lakes were compared to metals in Pumpkinseed *(Lepomis gibbosus)*, Black Crappie *(Pomoxis nigromaculatus)*, Brown Bullhead *(Ictalurus nebulosus)*, and Largemouth Bass *(Micropterus salmoides)*. Values for a species from different lakes were lumped together to increase sample size.

Mean zinc concentrations in muscle of the five species varied from 19.5 mg/kg in the Largemouth Bass to 67.6 mg/kg in the Brown Bullheads (Table 5). The highest concentration of zinc in liver occurred in Brown Bullheads. Zinc concentrations in liver of the other four species were somewhat similar (107-147 mg/kg).

Copper concentrations in muscle of the five species were similar, ranging from 0.87 mg/kg in Yellow Perch to 2.2 mg/kg in muscle of the Largemouth Bass (Table 6) Concentrations of copper in liver of the Black Crappie and Brown Bullheads were higher than in the other three species.

Cadmium concentrations in muscle were similar for the five species ranging from 0.32 to 1.1 mg/kg (Table 7). In liver, the range of values was from 3.8 to 24.5 mg/kg. Brown Bullheads contained the lowest concentrations of cadmium in muscle and in liver.

*Benthic insects:* Aquatic insects sampled from the bottom substrate of Anderson Lake were analyzed for metal concentrations (Table 8). Only Chironomids were obtained in large enough quantities for analysis at all three stations in the lake. Cadmium was below detection limits. Zinc and copper concentrations in the Chironomids decreased in insects collected at stations farther from the inlet, but not in direct correlation with the concentrations of zinc and copper in the sediments (Table 8).

TABLE 5. ZINC: Concentration of zinc in five species of fish from Coeur d'Alene River valley lakes.

| Species | Tissue | Mean Copper (mg/kg) | ± 95% C.I. | Range | N |
|---|---|---|---|---|---|
| Brown Bullhead (107) * | muscle | 67.6 | 6.5 | 18 to 262 | 19 |
| | liver | 232.1 | 17.9 | 122 to 426 | 12 |
| Yellow Perch (40) | muscle | 52.0 | 6.3 | 22 to 92 | 77 |
| | liver | 126.0 | 24.0 | 30 to 573 | 74 |
| Pumpkinseed (47) | muscle | 51.4 | 14.6 | 19 to 126 | 16 |
| | liver | 107.2 | 29.5 | 37 to 219 | 15 |
| Black Crappie (128) | muscle | 39.7 | 4.0 | 33 to 50 | 10 |
| | liver | 147.9 | 8.6 | 86 to 230 | 10 |
| Largemouth Bass (516) | muscle | 19.5 | 9.6 | 12 to 29 | 5 |
| | liver | 120.5 | 20.1 | 89 to 135 | 5 |

* ( ) average weight in grams
C.I. = Confidence Interval

*Cordulia* sp. (Libellulidae), a predacious dragonfly nymph, contained lower concentrations of zinc and copper than the other insects. However, *Chaoborus* sp., which is predacious on microcrustaceans and small insects, contained higher concentrations than the Chironomids.

TABLE 6. COPPER: Concentration of copper in five species of fish from Coeur d'Alene River valley lakes.

| Species | Tissue | Mean Copper (mg/kg) | ± 95% C.I. | Range | N |
|---|---|---|---|---|---|
| Brown Bullhead | muscle | 1.6 | 0.13 | 0.3 to 3.6 | 16 |
| (107)* | liver | 39.0 | 4.5 | 13 to 100 | 12 |
| Yellow Perch | muscle | 0.87 | 0.29 | 0.2 to 7.5 | 50 |
| (40) | liver | 16.5 | 7.3 | 1.7 to 110 | 32 |
| Pumpkinseed | muscle | 1.6 | 2.8 | 0.3 to 9.8 | 8 |
| (47) | liver | 8.8 | 2.6 | 3.8 to 15 | 10 |
| Black Crappie | muscle | 2.2 | 1.3 | 0.3 to 5.1 | 10 |
| (128) | liver | 41.3 | 4.5 | 5 to 81 | 10 |
| Largemouth Bass | muscle | 2.2 | 1.5 | 0.4 to 3.0 | 5 |
| (516) | liver | 18.6 | 10.4 | 5.3 to 29 | 5 |

*( ) average weight in grams
C.I. = Confidence Interval

TABLE 7. CADMIUM: Concentration of cadmium in five species of fish from Coeur d'Alene River valley lakes.

| Species | Tissue | Mean Copper (mg/kg) | ± 95% C.I. | Range | N |
|---|---|---|---|---|---|
| Brown Bullhead | muscle | 0.17 | — | 0.16 to 0.17 | 2 |
| (107)* | liver | 3.8 | 2.8 | 1.3 to 6.4 | 6 |
| Yellow Perch | muscle | 0.32 | 0.11 | 0.17 to 0.85 | 39 |
| (40) | liver | 16.1 | 5.6 | 1.6 to 36 | 49 |
| Pumpkinseed | muscle | 0.66 | 1.0 | 0.15 to 3.8 | 8 |
| (47) | liver | 11.6 | 5.4 | 2.3 to 33 | 11 |
| Black Crappie | muscle | 1.1 | 1.8 | 0.33 to 3.7 | 5 |
| (128) | liver | 24.5 | 4.0 | 4.9 to 55 | 10 |
| Largemouth Bass | muscle | 0.75 | 1.8 | 0.11 to 1.9 | 3 |
| (516) | liver | 12.7 | 10.3 | 4.2 to 28 | 5 |

*( ) average weight in grams
C.I. = Confidence Interval

TABLE 8. Zinc and copper in benthic insects and sediments from Anderson Lake, August 1973.

| Station* | Aquatic Insects | | | | Sediments |
|---|---|---|---|---|---|
| | Chironomidae | Libellulidae | Chaoborinae | Heleidae | |
| Zinc (mg/kg) | | | | | |
| 1 | 858 | 185 | — | — | 3250 |
| 2 | 216 | — | 538 | — | 3550 |
| 3 | 50 | — | — | 188 | 2150 |
| Copper (mg/kg) | | | | | |
| 1 | 52 | 37 | — | — | 76 |
| 2 | 13 | — | 66 | — | 87 |
| 3 | 20 | — | — | — | 34 |

*Station 1—inlet; stations 2 and 3—open water sites.

## Discussion

Dissolved metal concentrations in the lakes change seasonally with fluctuating water levels. In spring, large volumes of river water containing dilute metals enter the lakes. Zinc concentrations at this time ranged from <0.05 to 0.44 mg/1, and were highest near the inlets. Copper and cadmium concentrations were less than 0.02 mg/1. Once run-off ceases and suspended solids settle out, the concentration of zinc drops below detection limits (0.05 mg/1). During fall, as the water level drops in the river, dissolved metal concentrations increase, but concentrated metals do not enter the lateral lakes because water is flowing out the channels. This trend continues until winter rain or spring run-off again swells the river.

Zinc concentrations present in the lakes in the spring are probably not toxic to warm water species, but they may be toxic to trout. Becker and Thatcher (1973) tabulated a large number of bioassay studies concerning heavy metals. The 96-hour TLm for Bluegill, *Lepomis macrochirus,* estimated under various conditions, ranged from 1.9 to 20 mg/1 zinc. Bioassay estimates are generally on the lower end of this range for waters of low alkalinity such as the lateral lakes. Sappington (1969) found that the 96-hour TLm for Cutthroat Trout fingerlings in a static bioassay was only 0.09 mg/1 zinc. In the spring, zinc levels at the inlets are higher than the value reported by Sappington. However, trout may avoid these higher concentrations and move to the open water sites where zinc levels are lower. Salmonids exhibited an "avoidance reaction" to dissolved zinc in laboratory aquaria (Sprague, 1964; 1968)

High concentrations of zinc, copper, cadmium, lead, cesium, and antimony have been deposited in the surface sediments of the lakes. Concentrations were higher than measured in the control lake or reported as background. Funk *et al.* (1973) reported accumulation of metals to a depth of 70-80 cm. in the Coeur d'Alene Lake delta and 20-30 cm. in the lake proper. No measurement of deposition depths was made in the lateral lakes.

The distribution of metals in the sediments reflects the mode of deposition from the river. Lakes more intimately connected to the river contain higher concentrations of metals. Within a lake there is generally a gradient of decreasing metal concentrations outward from inlet stations.

Thomas (1972) found that mercury adsorbed to fine silty clays and organic sediments in greater amounts than it adsorbed to coarse inshore sediments. In the lateral lakes, the inlet stations contain larger quantities of sand as contrasted to the soft organic sediments at the open water stations. Thus, the composition of the sediments would tend to modify the general pattern of a decrease in metals at stations outward from the inlets.

Heavy metals may become stabilized in the sediments by the process of adsorption. Reimer and Toth (1970) observed that complete adsorption of 0.05 ppm $CuSO_4$ occurred in all sediment systems tested. The adsorptive capacity was related to clay and organic matter content. Thomas (1972) found that mercury was adsorbed by clays, sulfides, and hydrated iron oxides, and the concentration of mercury was positively correlated with organic carbon content. Quartz and sand did not adsorb mercury.

Not much information is available on the amounts of metals that can reenter water from the sediments. Maxfield and Wai (1971) demonstrated that a low equilibrium exists between water and sediment. They mixed Coeur d'Alene River sediments which

contained 3200-4700 mg/kg zinc with water at different pH levels. At a pH of 7.4, the saturation concentration for the water overlying the sediment was only 1.8 mg/1 zinc. The concentrations of zinc in the overlying water increased as the pH decreased. At pH levels found in the lateral lakes (Tables 1 & 2), dissolved zinc is maintained at low levels.

Although physical processes tend to keep metals in the sediments, biological processes may return them to the water column. For example, insoluble mercury is methylated by bacteria in the sediments and routed to fish via the water column or through the food chain (Jensen and Jernelow, 1969; Gillespie and Scott, 1971).

The sediments represent a storehouse of large amounts of metals which are potentially toxic to aquatic organisms. At neutral pH levels present in the lakes, the metals are essentially trapped in the sediments and do not enter the water column. Heavy metals are more soluble in water at low pH levels (Hem, 1972); consequently, any decrease in pH in the poorly buffered lakes could release the trapped metals.

In Table 9 the concentrations of metals in fish of the Coeur d'Alene lakes are compared to values reported in the literature for fish from other areas. All values were adjusted to mg/kg dry weight, and overall means were computed. The concentrations found in the Coeur d'Alene drainage fish are similar to the values reported for other studies. Only copper and cadmium in fish from the lateral lakes appear to be higher. However, this disparity may reflect inherent differences in the studies as well as an actual increase in concentration caused by metal pollution.

Based on comparison of amounts of metals to the control and to values reported for fish from other areas, it appears that zinc, copper, and cadmium have not accumulated to high levels in fish from the study lakes, even though these waters annually receive metals from the river. These and other studies have demonstratd that levels of zinc, copper, and cadmium in fish tissue may be a poor indicator of metal pollution.

Uthe and Bligh (1971) compared metals in fish from the Lower Great Lakes Basin, a highly industrialized area, to those from a nonindustrialized lake in Manitoba. Values for zinc, copper, and cadmium in liver tissue of Lake Whitefish, *Coregonus clupeaformis,* and Northern Pike, *Esox lucius,* were not significantly different between the two areas. Lucas *et al.* (1970) found that copper and zinc concentrations in 10 species of fish varied little among the Great Lakes. Cadmium concentrations did vary slightly with species among lakes, ranging from 0.06 to 1.4 ppm, wet weight.

Van Meter (1974) determined metal concentrations in salmonids, suckers, and sculpins from various sections of the Clark Fork River drainage in Montana. He observed little difference in zinc, copper, and cadmium concentrations between fish from locations unaffected by mining wastes and fish from those stretches exposed to mining effluents.

Among adult fish there appears to be a relationship between trophic level and zinc concentration in muscle. Marcusen (1966), in studying Round Lake, located in the same drainage as our study, found that Bullheads are omnivorous feeding on plankton, benthic insects, and plant matter; Yellow Perch, Pumpkinseed, and Black Crappie are largely carnivorous on plankton, benthic organisms, and surface insects; however, Largemouth Bass feed almost exclusively on fish. These species can be ranked generally according to trophic level from omnivorous to carnivorous in the following order: Brown Bullhead > Yellow Perch, Pumpkinseed, Black Crappie > Largemouth Bass. Zinc concentrations in muscle decreased along this rank from Brown Bullhead to Largemouth Bass

TABLE 9. Approximate averages of metals in fish reported in other studies, in mg/kg dry weight.

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| ZINC | — | 30 | 76.5 | 25.1 | 53.6 | ~10-100 | 52 | 138 |
| COPPER | 1.3 | 9 | 4.2 | 1.05 | 4.6 | ~1-8 | 1.2 | 23 |
| CADMIUM | .094 | 0.4 | —— | 0.15 | 0.53 | —— | 0.42 | 15 |
| TISSUE | wholefish Freshwater | liver | headless, dressed | noncarn. Flesh, Freshwater | muscle Osteichthyes marine | muscle, marine | muscle | liver |
| METHODS | Freezedried, ashed | | wet ashed, AAS | wet ashed, AAS | wet ashed, AAS | —— | wet ashed, AAS | |
| AUTHOR | Lucas *et al.*[a] 1970 | | Uthe & Bligh[b, c] 1971 | Mathis & Cummings[b] 1973 | Windom [c] *et al.* 1973 | Cross *et al.*[a,d] 1973 | present study | |

[a] mg/kg, ash weight

[b] Data reported as mg/kg (ug/g, ppm) wet weight was converted to mg/kg dry weight by multiplying by five (Lager, 1962, reported the average water content as 80%, so dry weight is approximately one-fifth of the wet weight).

[c] Overall average was approximated from data presented in publication.

[d] Derived from data points on a graph.

(Table 5). However, this trend was not evident in copper and cadmium concentrations (Tables 6 and 7).

Zinc concentrations may decrease in muscle from omnivorous species to predacious fish because of differences in metal content of the food they consume. An omnivorous fish feeds on detrital material, which is likely to contain high levels of metals. Among predacious fish, piscivores consume material that contains lower levels of metals than do fish which feed primarily on invertebrates.

Differences in metal concentrations among species may also be related to the size of the fish. Heavy metals, other than mercury, tend to decrease with an increase in size or age. Cross *et al.* (1973) observed either no change or a decrease in concentration of metals with increasing size in two marine species. O'Rear (1971) found a decrease in zinc and copper concentrations with size in Striped Bass, *Morone saxatilis*. The specimens of Largemouth Bass analyzed in this study were much larger in size than the other species.

In general, most metals have been shown to decrease at higher trophic levels. The few bottom invertebrates examined contained higher concentrations of zinc, copper, and cadmium than measured in fish fillets. Also, the omnivorous insects showed higher metal values than the predacious forms. Accumulation coefficients for manganese, copper, and zinc decreased from plankton to benthic organisms to fish in a marine food chain (Rozhanskaya, 1969). Windom (1973) also noticed a decrease in levels of zinc, copper, and cadmium from plankton to planktivorous fish in the ocean. Baptist and Lewis (1969) described the decrease of zinc-65 up an estuarine food chain. The concentration of copper, lead, and cadmium decreased from tubificids to clams to fish (fillet) in the Illinois River (Mathis and Cummings, 1973).

The most important factor in the relation of metals to food chains is probably the physiological differences in uptake and excretion rates among major groups of organisms. Concentration may occur by bioaccumulation, which is direct uptake from water; or by biomagnification, which is build-up via the food chain. If uptake of metals from water involves only passive diffusion, small organisms would be expected to have higher accumulation rates than larger organisms since accumulation would depend on the ratio of surface area to volume. Estimates of uptake rates may also be altered by adsorption. Cushing and Rose (1970) showed that uptake of zinc-65 in periphyton was dependent on an adsorptive mechanism.

Excretion of metals occurs in aquatic organisms, but little is known about the specific mechanism or rate for each metal (Pentreath, 1971). To maintain homeostasis, excretion must keep up with accumulation. If it does not, then storage into tissues will occur. Apparently homeostatic processes in fish from the lateral lakes are able to control metal concentrations at these exposure levels.

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# Vegetation Development on a Low Elevation Talus Slope in Western Montana

**Abstract**

Determinations of cover as a function of moss mat thickness and a shade index were used to infer the successional roles of species on talus slopes on the north side of a mountain in western Montana. Given a suitably inactive slope, the conversion of the originally xeric conditions into a more mesic environment probably occurs through the development of a moss mat *(Tortula ruralis, Homalothecium aeneum,* and *Dicranum scoparium)* followed by a *Pseudotsuga menziesii* — shrub community. Although lichens pioneered the slopes, their contribution to the succession, if any, was unknown. Mat development originated in the rock interstices, while those moss species growing on rock surfaces (*Grimma* spp.) apparently were inconsequential in succession.

## Introduction

Talus slopes are common in mountainous areas, but little attention has been given to primary plant succession occurring on these slopes. Important vascular plant species associated with succession on talus in one location in the northern Rocky Mountains have been defined (Daubenmire and Slipp, 1943). However, changes in abundance of moss and lichen species involved apparently have not been previously studied in the United States, and the vascular plants occurring on talus at low elevations in western Montana differ considerably from those found by Daubenmire and Slipp. In this study, abundance of plant species, mat thickness, and shade were measured and interspecific associations determined in order to aid the description of the succession.

Talus slopes are the result of the accumulation of rock fragments fractured by weathering and mass wasting of bedrock (Thornbury, 1954). The terms talus and scree are generally used synonymously for the material comprising these slopes.

In northern Idaho, Daubenmire and Slipp (1943) described plant succession on talus on the north and south aspects of a ridge. Succession on the north exposure was significantly initiated by development of a moss mat from the interstices between rocks followed by herbs, shrubs, and finally an *Abies lasiocarpa-Menziesia ferruginea* forest association. On the south exposure, succession proceeded from the margins of the talus slope first by encroachment of the low-matted perennial, *Eriogonum subalpinum,* which was typically followed by the establishment of a *Festuca idahoensis-Agropyron spicatum* grassland association. Differences in snow accumulation and surface temperatures acting through soil moisture were believed to be responsible for the successional and climax vegetation differences on the two contrasting aspects.

Primary plant establishment and community development on fixed bare rock have been studied more thoroughly (Cooper, 1912; Whitehouse, 1933; Oosting and Anderson, 1937 and 1939; Keever *et al.,* 1951), and are similar to primary succession on talus, particularly in the successional trend toward a mesic habitat through the development of an organic mat over the rock surface.

### The Study Area

The study area was located 3.2 km due east of Missoula in Lolo National Forest of western Montana near the base of the north side of University Mountain (46°52′N, 113°57′W) at an elevation of 1060 m. The general topography consists of a steep but shallow system of ravines and ridges bordering the south side of the east-west trending, flat-bottomed Clark Fork River valley, which at this point is narrow (0.5 km). A semi-arid climate prevails, with an average annual precipitation of 36 cm. Average January and July temperatures are –5.4°C and 19.8°C, respectively.

*Pseudotsuga menziesii* is normally the climax dominant on the north side of University Mountain. However, *Pinus ponderosa, Agropyron spicatum,* and *Festuca scabrella* share the climax dominance to a degree on the drier slopes and ridges in the study area.

The area has not burned recently, although scattered *Larix occidentalis* indicate that fire was probably part of the area's past.

Noncalcareous Precambrian sedimentary rocks showing various degrees of slight metaporphism predominate in the study area, while diabasic igneous rocks are locally common. Numerous bedrock outcrops usually less than 10 m high feed the talus slopes that cover most of the remaining area. The talus surface was usually from zero to 20 cm below the surface of the slope. The blocks generally range from 5 cm to 25 cm in diameter and show various degrees of sorting, the larger fragments being farther from the source cliff. The slope ranges from 23° to 37° from the horizontal with most values falling between 30° and 35°.

### Methods

The sample consisted of forty-five 0.5 m X 1.0 m quadrats randomly spaced along a 530 m transect following an elevational contour (1060 m) and spanning three steeply sloping ridges. Only those quadrats with an exposure between W and 35° N of W were included, in order to insure that sampling was confined to a reasonably uniform exposure.

At each quadrat position, slope, aspect, shade, mat thickness, and plant cover were measured. Areas covered by mosses, macrolichens, and *Sedum* were estimated to the nearest $dm^2$ for each species. Herbaceous plants other than *Sedum* and grasses were not included in this study as sampling was begun in the spring before most herbaceous plants appeared. The densities of tree and shrub species were approximated by compiling density estimates for each species in three categories representing distances from the quadrat. The categories were x) directly above or in the quadrat, y) within 1 m of the quadrat, and z) between 1 m and 3 m from the quadrat. Each species in each position category was assigned an integer between zero and three inclusive, representing densities from "absent" to "abundant". The final density estimate (d) for each species for each quadrat was obtained by summation of the weighted estimates from each position category. The categories were weighted by factors of 3, 2, and 1 respectively ($d = 3x + 2y + z$). The closer categories were weighted more heavily as it was assumed that the closer the trees and shrubs were to the quadrat, the greater would be their effects on the plants in the quadrat. For a given species in a given quadrat, the sum of the weighted estimates for each position category equals the density index.

A shade index for each quadrat was derived by summing the density indices of the trees and shrubs at that quadrat. The density indices for *Symphoricarpos albus* were halved before inclusion in the sums as a correction for relatively small size.

Mat thickness within each quadrat was estimated by averaging 33 regularly spaced measurements. These were made by insertion of a rigid calibrated wire until contact was made with rock. The term "mat" includes living mosses as well as underlying humus.

Probable successional roles of species were inferred by examination of cover *v.* mat thickness and cover v. shade index functions. These roles were further elucidated by field observation and analysis of interspecific associations. Correlation coefficients were calculated for all possible pairs of species as a test for the existence of associations. The cover and density values were not assumed to be normally distributed. Normal distributions were unnecessary as the correlation coefficient was merely being used as a test for the existence of association rather than as a measure of association inferring a true linear relationship (Grieg-Smith, 1964).

Nomenclature of lichens and mosses follows the lists of Hale and Culberson (1970) and Crum *et al.* (1973) respectively, whereas vascular plant names follow Hitchcock and Cronquist (1973). *"Cladonia chlorophaea"* was used in a conservative sense due to the impossibility of field separation of chemical variants.

Voucher specimens of bryophytes and lichens were deposited in the University of Montana Herbarium, Missoula, Montana.

**Results and Discussion**

*The talus environment:* A bare talus slope is inhospitable to most plants not only because it is unstable, but also because it is very dry and lacks available nutrients. Instability is disadvantageous to colonization by plants as suitable conditions for colonization occur infrequently, and those colonies that do start are always faced with the possibility of destruction (Leach, 1930). Because there is no soil, precipitation is virtually unavailable, most of the water either evaporating or rapidly percolating from the surface.

It should be borne in mind that successful plant invasion is dependent upon geomorphic processes as at least some degree of slope inactivity is required to allow establishment of plants in the interstices between rocks (chomophytes). Both slow (talus creep) and fast (debris slides) movements occur on talus slopes, and fast movements are relatively important as a habitat factor. Forces such as falling rocks, precipitation, expansion and contraction due to temperature changes, frost wedging, and animals also contribute to talus movements (Carson and Kirkby, 1972).

Vegetation patterns on talus appear to be closely related to patterns of rockfall accumulation and movement, successful plant invasion occurring primarily where there is little accumulation or movement. Sheltered areas usually occur downslope of bedrock outcrops of all sizes. Large cliffs typically have a strip of a relatively mature community immediately downslope. This feature probably occurs because most rock fragments falling from a cliff are of such a size that the momentum gained in falling carries them well beyond the base of the outcrop. Falling debris is often channeled into narrow, sharply defined chutes supporting little or no vegetation. Predominantly small fragments compose the material being deposited immediately below the cliff; in this case, the quantity is usually small enough to have an insignificant effect on the community at the base of the outcrop. However, in areas where a greater volume of small fragments is being released, the slope stability at the base of the outcrop could be greatly diminished to the point of prevention of colonization.

The slope stability required for colonization will often arise in the normal processes of weathering and mass wasting of bedrock. Maintenance of an active slope is dependent upon addition of talus from above unless the talus is being removed from below. When the supply of rocks is cut off due to the eventual disappearance of feeding outcrops or changing patterns of rockfall movement, the slope activity decreases, allowing pioneers to establish themselves.

When, on a geologic time scale, a slope has become suitably stable, the original xeric environment may be converted, through plant invasion, into a more mesic environment with a coincident increase in mat thickness.

*Vegetation on talus:* Figure 1 depicts for each species the mean cover/quadrat (mean density index/quadrat for trees and shrubs) as a function of mat thickness and shade index classes for west exposures. Only species occurring in more than five quadrats were included. The sample distribution with respect to mat thickness and shade index is also included.

Species tended to be differentially distributed with respect to the two environmental factors, mat thickness and shade, as indicated in Figure 1. However, there was a high degree of variability in the response of many species to shade and mat thickness. Contributing factors probably included variability in slope, aspect, bedrock composition, dissemination of reproductive bodies, fire history, position relative to the "drip zone" of trees (Tamm, 1950), and position with respect to ridges and ravines (microclimatic defferences), as well as experimental error and inadequacies of the semi-subjective shade index as a measure of shade. The species' responses were further obscured by the fact that important variations in habitat factors were occasionally distinctly patterned over areas smaller than the quadrat size.

Cover, as a function of mat thickness and shade index, indicated to a degree a given species' role in the succession, as both mat thickness and the shade index tend to increase during successional development. However, as the community develops, mat thickness appears to become a less reliable indicator of the maturity of a talus community, partly due to a weakening of the relationship between mat thickness and the water retaining capability of the mat. This fact is partly due to differences in the growth forms of the mosses comprising the mat. For instance, *Rhytidiadelphus triquetrus* tends to form wefts (loosely intertwined shoots and branches), while *Dicranum scoparium* forms denser turfs (parallel upright shoots) with a greater capacity to hold water (growth form terminology from Gimingham and Birse, 1957). Also, with successive increases in mat thickness, additional increments of thickness become relatively less important in the relief of moisture stress. Mat thickness may be overcome in importance by other factors, such as canopy development, as the community matures.

Significant positive interspecific associations are shown in Figure 2. Each species is represented by a point, the position of the point determined by the mean mat thickness and mean shade index for that species. Significant positive associations are shown by lines connecting the points representing the species involved. It can be seen from this figure that there is a tendency for species with similar mean mat thickness and/or shade indices to be positively associated. This diagram also roughly depicts the possible temporal relationships between species, succession apparently proceeding from the lower left to the upper right.

Primary succession appears to be strongly dependent upon mat development on

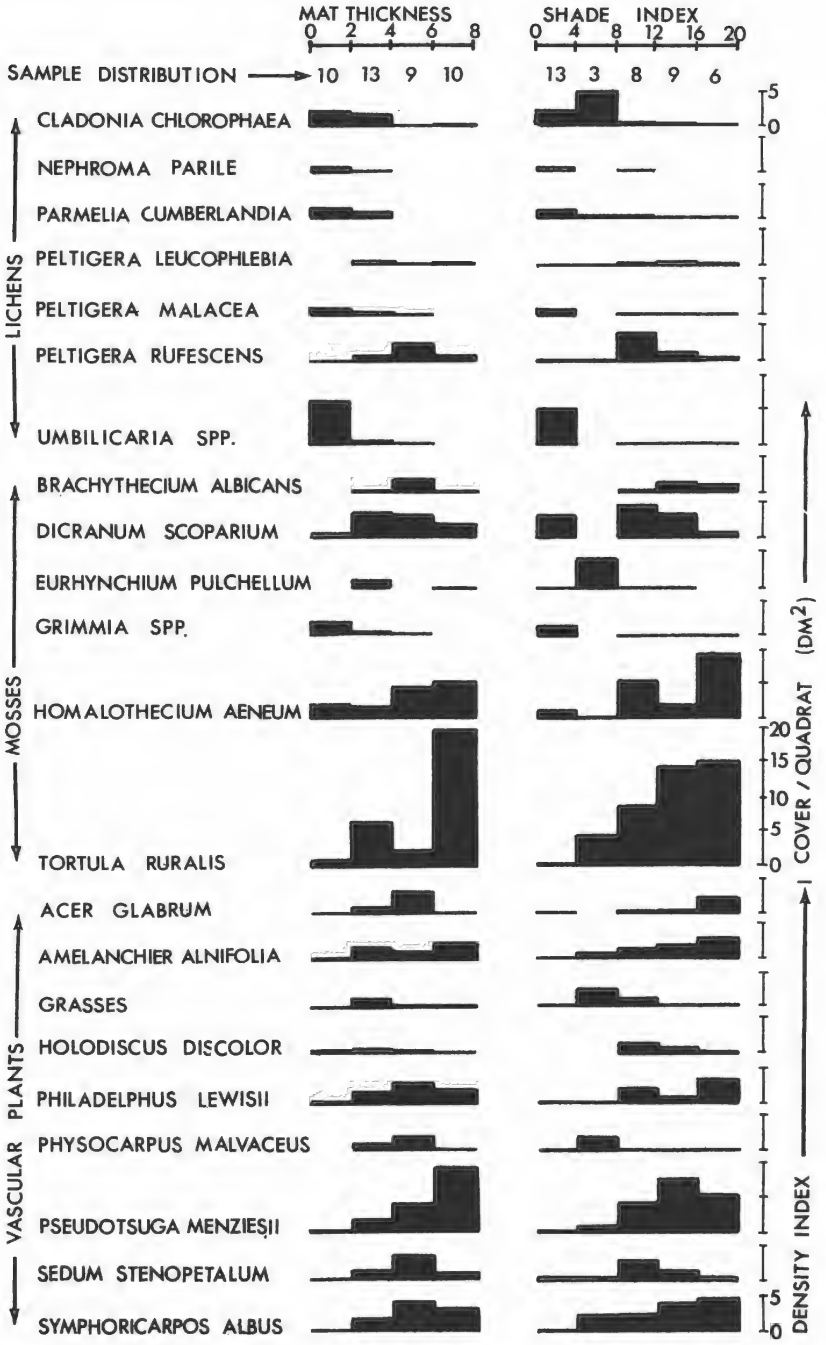


Figure 1. Cover of species ($dm^2$/quadrat for mosses and lichens, mean density index/quadrat for trees and shrubs) as a function of mat thickness and shade index.

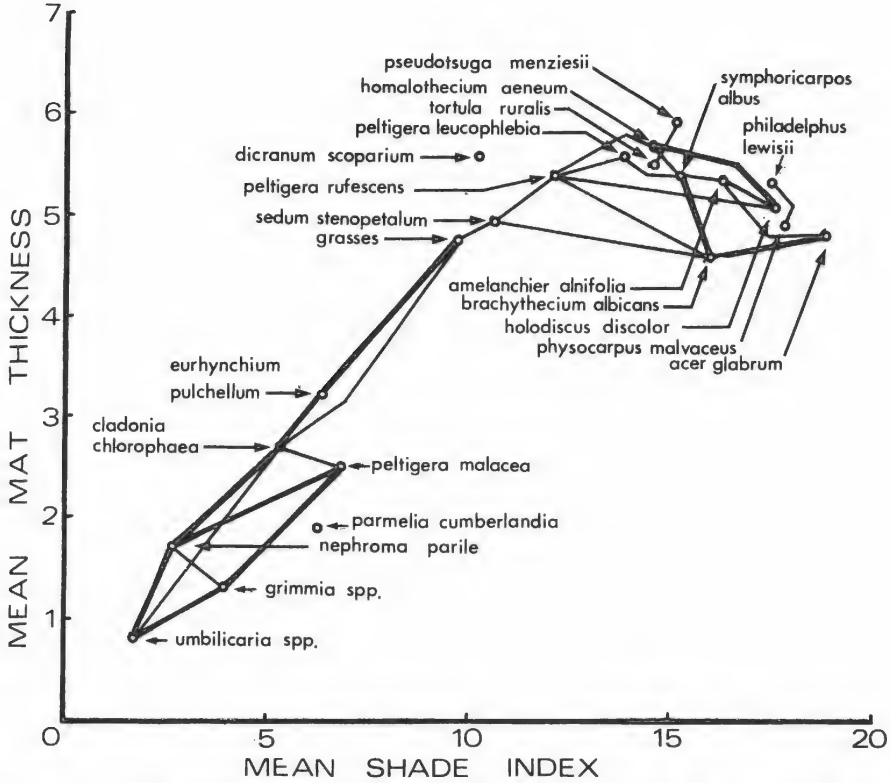


Figure 2. Positive interspecific associations. Heavy and light lines indicate significance at the .005 and .05 levels, respectively. Each species is represented by a point, the position of the point determined by the mean mat thickness and mean shade index for that species.

talus slopes (Daubenmire and Slipp, 1943), as well as on fixed bare rock (Whitehouse, 1933; Oosting and Anderson, 1937 and 1939; Keever *et al.,* 1951).

*Successional relationships of species:* The following paragraphs and Table 1 outline the general hypothetical pattern of succession found on the north side of University Mountain. However, the pattern is not entirely unique to University Mountain, and is similar to the patterns described by Leach (1930) in Great Britain, and by Daubenmire and Slipp (1943) on north exposures in northern Idaho. While the species differ, similarities in the growth forms and genera exist.

The successional and pedogenic importances of crustose lichens are controversial. In a thorough review of the subject, Syers and Iskandar (1973) stated that while the successional and soil-forming importance of crustose lichens was emphasized in the early literature, twentieth century workers have taken the other extreme. Recent evidence has led Syers and Iskandar to conclude that lichens may possibly play an important role in soil formation and plant succession, contrary to the general consensus (Oosting and Anderson, 1937 and 1939; Keever *et al.,* 1951; Daubenmire and Slipp, 1943).

Lichens have been shown to aid in the decomposition of rock mechanically via expansion and contraction of the thallus and penetration of rhizines (Fry, 1927). Chemically, lichens promote rock decomposition through solution (especially in limestone) and chelation of metal ions by slightly soluble lichen compounds, particularly depsides and depsidones, forming water-soluble metal complexes (Syers and Iskandar, 1973).

Over geologic time, lichens may contribute significantly to soil formation, although the amount formed on a successional time scale would contribute little to the relief of the moisture stress of the habitat. It seems more likely that on relatively resistant rock, crustose lichens may play an important role by accumulating essential nutrients (particularly phosphorus) and converting them to forms available to higher plants (Syers and Iskandar, 1973).

The first mosses to appear, the lithophytes *Grimmia affinis, G. montana,* and occa-

TABLE 1. Generalized hypothetical sequence of invasion.

I. Lithophytic Pioneers
- Lichens
  - *Alectoria pubescens*
  - *Candelariella vitellina*
  - *Dimelaena oreina*
  - *Lecanora chrysoleuca*
  - *L. cinerea*
  - *L. melanophthalma*
  - *L. muralis*
  - *L. rupicola*
  - *Lecidea atrobrunnea*
  - *L. insularis*
  - *L. pantherina*
  - *Nephroma parile*
  - *Parmelia cumberlandia*
  - *P. disjuncta*
  - *P. plittii*
  - *P. saxatilis*
  - *Rhizocarpon grande*
  - *Umbilicaria hyperborea*
  - *U. polyphylla*
  - *U. torrefacta*
- Bryophytes
  - *Grimmia affinis*
  - *G. calyptrata*
  - *G. montana*
  - *Rhacomitrium heterostichum*

II. Chomophytic Pioneers
- Lichens
  - *Cladonia cornuta*
  - *C. ecmocyna*
  - *C. multiformis*
  - *C. phyllophora*
  - *Stereocaulon alpinum*
- Bryophytes
  - *Dicranum muehlenbeckii*
  - *D. scoparium*
  - *Homalothecium aeneum*
  - *Hylocomium splendens*
  - *Lobbozia barbata*
  - *Polytrichum juniperinum*
  - *Tortula ruralis*
- Vascular Plants
  - *Selaginella wallacei*

III. Secondary Chomophytic Invaders
- Lichens
  - *Cladonia chlorophaea*
  - *C. fimbriata*
  - *C. pyxidata*
  - *Diploschistes scruposus*
  - *Peltigera malacea*
  - *Polychidium muscicola*
  - *Psoroma hypnorum*
  - *Stereocaulon albicans*
- Bryophytes
  - *Bryum caespiticium*
- Vascular Plants
  - *Agropyron spicatum*
  - *Cystopteris fragilis*
  - *Festuca idahoensis*
  - *Heuchera cylindrica*
  - *Koeleria cristata*
  - *Poa* sp.
  - *Sedum stenopetalum*
  - shrub seedlings
  - *Woodsia oregana*

IV. *Pseudotsuga*-Shrub Association
- Lichens
  - *Peltigera leucophlebia*
  - *P. rufescens*
- Mosses
  - *Dicranum scoparium*
  - *Homalothecium aeneum*
  - *Hylocomium splendens*
  - *Mnium venustum*
  - *Rhytidiadelphus triquetrus*
  - *Timmia austriaca*
  - *Tortula ruralis*
- Vascular Plants
  - *Acer glabrum*
  - *Amelanchier alnifolia*
  - *Holodiscus discolor*
  - *Philadelphus lewisii*
  - *Physocarpus malvaceus*
  - *Pseudotsuga menziesii*
  - *Ribes* spp.
  - *Symphoricarpos albus*

sionally *Rhacomitrium heterostichum* var. *heterostichum,* generally appeared to follow the lichens listed above, although Keever *et al.* (1951) found that colonization of *Grimmia laevigata* does not require previous lichen colonization. Even though cushions of *Grimmia* do collect small amounts of soil, it is unlikely that they make an important contribution to the succession because they tend to grow on rock surfaces (lithophytic) rather than in the interstices between the rocks (chomophytic). Chomophytes play an important role in succession on talus by successfully invading interstices and relatively inactive regions of the slopes.

The foliose lichen *Peltigera malacea* was often found growing over cushions of invading chomophytic mosses. Due to its ability to fix nitrogen, it may be important in nutritional aspects of succession.

On drier sites, *Selaginella densa* and *S. wallacei* were frequently chomophytic pioneers and seemed particularly effective in binding small rock fragments at the surface.

The moss mat originates in the interstices, and the surrounding rock faces are gradually covered by the expanding mosses, eventually forming a continuous carpet over the talus. Vascular plants become established by using the moss mat for germination and seedling development (Daubenmire and Slipp, 1943). Shrubs in turn further the trends toward stability, a thickened mat, and increased mesophytism. The means by which shrubs promote these trends are probably a combination of the following: providing shade, adding to the total quantity of organic matter in the mat, and stabilizing the talus with their root systems. Of the shrubs, only *Holodiscus discolor* was more abundant in relatively xerophytic immature communities.

*Pseudotsuga menziesii* becomes established, often in the shade provided by shrubs and adjacent colonized areas, and later develops into the climax dominant.

Populations of *Populus tremuloides* and *P. trichocarpa* were frequently found at the base of talus slopes and occasionally on the slopes. Presumably these trees take advantage of locally plentiful ground water and seem relatively insensitive to the instability of the site. Perhaps this occurence is a reflection of adaptations to the recurrent disruptions in their more usual habitats along rivers and streams.

*Rate of succession:* It was assumed throughout this study that the observed patterns in the vegetation were a result of succession. As this assumption seems reasonable, no direct proof of a temporal relationship between communities was sought. Given the above assumption, certain conclusions concerning successional rates were made.

Talus slopes were commonly encountered that were lichen-covered, yet were not being actively fed by talus. The fact that the slopes had not been invaded by more mesophytic species, yet were inhabited by large (often 10 cm in diameter), slow-growing (radial growth probably between 0.3 and 2.0 mm/yr) crustose lichens, indicates that the conversion of a xeric to a mesic habitat is slow and lags behind the availability of a suitable slope.

Consideration of rockfall rates provides a useful means for appreciating the slow pace of plant invasion. Carson and Kirkby (1972) listed rates of rock wall retreat at various locations and with various rock types as falling between 0.04 and 0.50 mm/yr. From these figures it can be calculated that a cliff face 1 m wide by 10 m high would release a volume of rock between 400 $cm^3$ and 5000 $cm^3$ per year, equivalent to a cube between 7.4 and 17 cm on a side. Considering this slow rate of deposition and the fact that relatively bare talus slopes are common, as are intermediate stages in the sere,

the rate of succession must also be very slow. Otherwise, more talus slopes with the potential of developing into a more mesophytic habitat would have realized that potential.

Successional rates near zero may occur on some slopes, given an equilibrium between the instability of the talus or other environmental factors and the attempts at colonization. Thus, a slope could be stable enough to support some chomophytes, but not stable enough to allow significant development of the chomophytes and followers. Other environmental factors such as dryness may play a role in the indefinite maintenance of an early successional stage (Daubenmire and Slipp, 1943).

Successional rates are probably higher in smaller areas of talus, due to a greater circumference to area ratio. Edges promote succession through the sheltering effect of the surrounding trees and shrubs (Daubenmire and Slipp, 1943) as well as through increased contributions of organic matter to the developing mat.

Differences in the abundance of immature talus communities between north and west exposures imply that, in general, successional rates are faster on north exposures than on west exposures. Mats in general appeared to be deeper on north slopes, and relatively bare talus was apparently more frequent on west exposures. Although these differences may be a result of directional differences in rates of mass wasting of bedrock, it seems more than likely that successional rates are considerably slower on west exposures due to less favorable moisture conditions on west-facing slopes. Thus, the rate of succession appears to be dependent upon the general favorability of the habitat to the growth and reproduction of relatively mesophytic plant species.

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# Checklist and Relative Abundance of Fish Species from the Hanford Reach of the Columbia River

**Abstract**

A checklist of fish species collected in over 30 years of research is presented for the Columbia River adjoining the U.S. Energy Research and Development Administration's Hanford Reservation (km 550-629), southcentral Washington. Differences in species composition and relative abundance within the area are discussed.

## Introduction

Several sources list fish species inhabiting various parts of the Columbia River system (Schultz and DeLacey, 1935; Schultz, 1936; Roebeck *et. al.,* 1954; Davis *et. al.,* 1956; Miller, 1959; McPhail, 1967; Reimers and Bond, 1967; Eddy, 1969; Patten *et. al.,* 1970). Although fisheries scientists have collected information on resident and anadromous fishes for over 30 years, little quantitative data have been published regarding the majority of species inhabiting the Columbia River adjoining the Energy Research and Development Administration's Hanford reservation in southcentral Washington.

The Columbia River adjoins the Hanford reservation beginning about 10 km (6 miles) north of Richland, Washington, between river kilometers (km) 550 and 629, and between river miles (rm) 343 and 393 (Fig. 1). The Hanford reservation is a unique area because of its closure to the general public since 1942 by federal regulations. Furthermore, it contains the last free-flowing stretch of the Columbia River remaining above Bonneville Dam.

Most early fishery investigations in the Hanford area were concerned with salmonids in association with potential thermal, chemical and radiation impacts from the operation of up to nine plutonium production reactors during World War II and until 1971. In recent years, assessment studies for future siting of nuclear power plants at Hanford have required extensive collections of all fish species. This article lists the fish fauna, relying mainly on data collected during 1973-1975 at two different Hanford locations. Less common species collected earlier by other workers from sites within the Hanford area are included to provide a composite list.

## Methods and Materials

From April, 1973, to June, 1974, fish were sampled weekly between Columbia River km 605 and 613 (rm 378-383). In September, 1974, sampling began between km 557 and 566 (rm 348-354) and continued at intervals of about three weeks. After collection, species were identified by using standard taxonomic keys (Schultz, 1936;

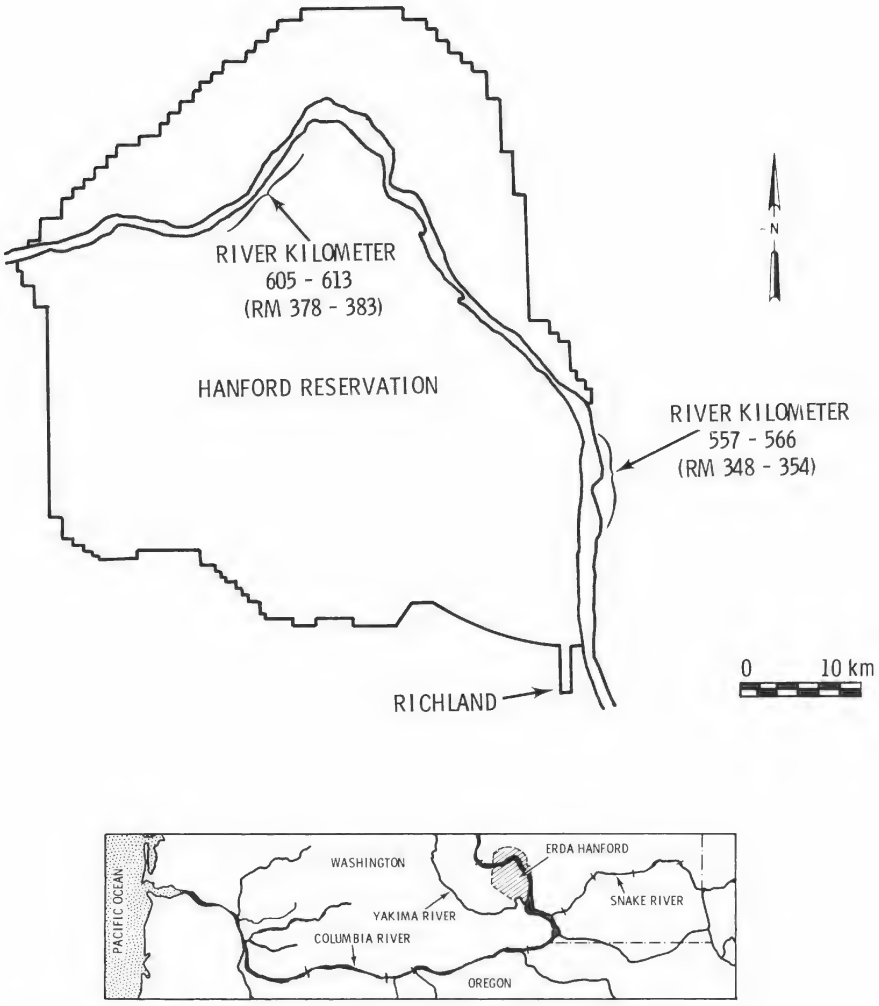


Figure 1. Location of the ERDA Hanford Reservation and fish sampling locations.

Carl *et. al.,* 1967; Eddy, 1969; Bond, 1973). Questionable identifications were confirmed by taxonomists and fisheries biologists having extensive experience with Columbia River fishes (C. D. Becker and D. G. Watson, Battelle Northwest Laboratories; C. E. Bond, Oregon State University). To insure taxonomic consistency, selected specimens were preserved in 5 percent formalin and maintained in a reference collection.

Several types of sampling gear and methods were used to suit various areas and to compensate for gear selectivity. Methods included: gill nets, trammel nets, beach seines, hoop nets, minnow traps, trotlines, electroshocker, various types of trawls, and hook and line. Some species were collected from the traveling screens of a water intake structure at Columbia rm 380 (Gray, Page, Wolf, and Schneider, 1975; Page, Gray,

and Wolf, 1975). The resulting species list was derived from all the above methods. However, only gill nets, hoop nets, and beach seine collections provided relative abundance data for one complete annual cycle at the two sampling sites.

Gill nets were set from shore into the river or were set offshore perpendicular to the current in deeper waters, and were rotated among various locations at each study area. Nets were about 2 m (6-8 ft.) deep and composed of panels of different mesh size ranging in 1.25 cm (0.5 in.) increments, from 1.25-10 cm (0.5-4 in.) square-mesh. Nets varied in length from 7.5-37.5 m (25-125 ft.). Net length was dependent on location and hydrological conditions of the river at the time of set. Gill nets were set in the afternoon and retrieved the next morning about 19 hours later.

Hoop nets were usually set for 1 week periods, checked every 24-72 hours, and rotated among various locations. Hoop nets were composed of two 61 cm (24 in.) diameter tunnels, each 3 m (10 ft.) long and set in pairs so the mouth of one tunnel faced the mouth of the second. Each tunnel was supported by 6 hoops with throats attached on the first and third hoop. The two tunnels were connected with a lead, 61 cm (24 in.) high and 6 m (20 ft.) long. Mesh size of the throats, netting surrounding the hoops and connecting lead, was 1.25 cm (0.5 in.) square mesh.

Beach seining was done at four locations on both sides of the river at each study site. Seining encompassed about 30 m (100 ft.) of shoreline at each location. The seine was 1.2 m (4 ft.) deep, 9 m (30 ft.) long and consisted of 0.32 (⅛ in.) mesh.

Catch per unit effort (C/UE) of fish collected by gill net, hoop net, and beach seine was calculated as follows: Gill net C/UE was the average number of fish caught per overnight set (about 19 hours) of 33 m (100 ft.) of net. Hoop net C/UE was the average number of fish caught per 24 hours set. Beach seine C/UE was the average number of fish caught per beach seine haul.

#### Results and Discussion

Forty-three species of fish representing 13 families have been collected since 1943 in the Columbia River adjoining the Hanford Reservation (Table 1). These include mainly resident, but also anadromous (Clupeidae, Petromyzontidae, Salmonidae) forms.

Thirty-seven species of fish representing 12 families were collected at river km 557-566 and 605-613 in 1973-75. Thirty-one species were collected at km 605-613 and 34 species at km 557566.

Differences in species lists between the up and downriver sites were attributable to the presence or absence of various species. Mottled sculpin *(Cottus bairdi)*, reticulate sculpin *(C. perplexus)* and leopard dace *(Rhinichthys falcatus)* were only collected at km 605-613. Mountain sucker *(Catos tomus platyrhynchus)*, smallmouth bass *(Micropterus dolomieui)*, largemouth bass *(M. salmoides)*, black bullhead *(Ictalurus melas)*, yellow bullhead *(I. natalis)*, and walleye *(Stizostedion vitreum)* were only collected at km 557-566. Differences between the two sites are somewhat relative. Fish move up and downriver and all species may be present at both sites at some time during the year.

At the upriver site, resident redside shiner *(Richardsonius balteatus)*, northern squawfish *(Ptychocheilus oregonensis)*, largescale sucker *(Catostomus machrocheilus)* and the anadromous chinook salmon *(Oncorhynchus tshawytscha)* were caught in near equal numbers and collectively comprised 90 percent of the total catch.

TABLE 1. Composite list of fish species by family collected at Columbia River km 605-613 from March, 1973, through June, 1974; km 557-566 from September, 1974, through September, 1975, and elsewhere on the Hanford Reservation.

| Family | Scientific Name | Common Name | Sample Location | | Other Hanford Sites |
|---|---|---|---|---|---|
| | | | KM 605-613 | KM 557-566 | |
| Acipenseridae-Sturgeons | *Acipenser transmontanus* Richardson | White sturgeon | X | X | |
| Catostomidae-Suckers | *Catostomus columbianus* Eigenmann & Eigenmann | Bridgelip sucker | X | X | |
| | *C. macrocheilus* Girard | Largescale sucker | X | X | |
| | *C. platyrhynchus* Cope | Mountain sucker | | X | |
| Centrarchidae-Bass and Sunfish | *Lepomis gibbosus* Linnaeus | Pumpkinseed | X | X | |
| | *L. macrochirus* Rafinesque | Bluegill | X | X | |
| | *Micropterus dolomieui* Lacepede | Smallmouth bass | | X | |
| | *M. salmoides* Lacepede | Largemouth bass | | X | |
| | *Pomoxis annularis* Rafinesque | White crappie | | | X[1] |
| | *P. nigromaculatus* Leseur | Black crappie | X | X | |
| Clupeidae-Herrings | *Alosa sapidissima* Wilson | American shad | X | X | |
| Cottidae-Sculpins | *Cottus asper* Richardson | Prickly sculpin | X | X | |
| | *C. bairdi* Girard | Mottled sculpin | X | | |
| | *C. beldingi* Eigenmann & Eigenmann | Piute sculpin | X | X | |
| | *C. perplexus* Gilbert & Evermann | Reticulate sculpin | X | | |
| | *C. rhotheus* Smith | Torrent sculpin | X | X | |
| Cyprinidae-Minnows and Carps | *Acrocheilus alutaceus* Agassiz & Pickering | Chiselmouth | X | X | |
| | *Cyprinus carpio* Linnaeus | Carp | X | X | |
| | *Mylocheilus caurinus* Richardson | Peamouth | X | X | |
| | *Ptychocheilus oregonensis* Richardson | Northern squawfish | X | X | |
| | *Rhinichthys cataractae* Valenciennes | Longnose dace | X | X | |
| | *R. falcatus* Eigenmann & Eigenmann | Leopard dace | X | | |
| | *R. osculus* Girard | Speckled dace | X | X | |
| | *Richardsonius balteatus* Richardson | Redside shiner | X | X | |
| | *Tinca tinca* Linnaeus | Tench | | | X[1] |

TABLE 1 (Continued)

| | | | | | |
|---|---|---|---|---|---|
| Gadidae-Codfishes | *Lota lota* Linnaeus | Burbot | | | X[1,2,3] |
| Gasterosteidae-Sticklebacks | *Gasterosteus aculeatus* Linnaeus | Threespine stickleback | X | X | |
| Ictaluridae-Freshwater Catfishes | *Ictalurus melas* Rafinesque | Black bullhead | | X | |
| | *I. natalis* Leseur | Yellow bullhead | | X | |
| | *I. punctatus* Rafinesque | Channel catfish | X | X | |
| Percidae-Perches | *Perca flavescens* Mitchell | Yellow perch | X | X | |
| | *Stizostedion vitreum* Mitchell | Walleye | | X | |
| Percopsidae-Troutperches | *Percopsis transmontana* Eigenmann & Eigenmann | Sand Roller | X | X | |
| Petromyzontidae-Lampreys | *Entosphenus tridentatus* Gairdner | Pacific lamprey | X | X | |
| | *Lampetra ayresi* Gunther | River lamprey | | | X[2] |
| Salmonidae-Salmon, trout, whitefish | *Coregonus clupeaformis* Mitchell | Lake Whitefish | | | X[1] |
| | *Oncorhynchus kisutch* Walbaum | Coho salmon | X | X | |
| | *O. nerka* Walbaum | Sockeye salmon | X | X | |
| | *O. tshawytscha* Walbaum | Chinook salmon | X | X | |
| | *Prosopium williamsoni* Girard | Mountain Whitefish | X | X | |
| | *Salmo clarki* Richardson | Cutthroat trout | | | X[1] |
| | *S. gairdneri* Richardson | Rainbow trout (steelhead) | X | X | |
| | *Salvelinus malma* Walbaum | Dolly Varden | X | X | |

[1] D. G. Watson (personal communication).
[2] C. D. Becker (personal communication).
[3] M. P. Fujihara (personal communication).

At the downriver site, chinook salmon comprised 44 percent of the catch and resident peamouth chub *(Mylocheilus caurinus)*, largescale sucker, northern squawfish, mountain whitefish *(Prosopium williamsoni)*, bridgelip sucker *(Catostomus columbianus)*, chiselmouth *(Acrocheilus alutaceus)*, and redside shiner comprised another 49 percent. The larger numbers of chinook salmon at km 557-566 were 0-age juveniles, occurring seasonally near shore and collected by beach seine. These fish reflect the occurrence of major salmon spawning areas between km 566 and 602 (Watson, 1974), the shoreline orientation of downstream migrants (Mains and Smith, 1964), and our shore-oriented sampling methods.

To better compare species composition at the two collecting locations, species and C/UE of gill nets, hoop nets, and beach seines were evaluated for the same months of the year at each location (Table 2). Although sampling occurred in different years, these methods were used for one annual cycle at each site. For assessment purposes,

comparisons were made for the periods June, 1973, through May, 1974, at km 605-613; and October, 1974, through September, 1975, at km 557-566.

A comparison of methods shows a difference in vulnerability of each species at different stages in its life cycle. However, the composite catch from gill nets, hoop nets, and beach seines provides a good representation of the species, sizes and life stages of fish present. We used this data to derive a numerical value of average relative abundance or a relative abundance index (RAI). We based the RAI on the average of three annual C/UE values for each species at each collecting site (Table 2). Species collected at the upriver location between km 605-613 are listed in descending order of abundance or rank. The rank of species collected at the downriver location between km 557-566 is shown in Table 2 parenthetically next to the RAI for that species.

Although small differences in C/UE are insignificant, analysis shows that species composition and relative abundance of some collected fish differ between the two sites. The difference may reflect our inability to sample equally all habitats, annual differences in river temperatures and flows, or habitat differences in the Columbia River adjoining the Hanford reservation.

There are several obvious differences between the two sites. The upriver sample area is a straight and deep channel with no islands, a maximum depth of 10 m and few shoreline indentations. The bottom consists mainly of boulders and large rock over 10 cm in diameter. The channel at the downriver site is shallower, wider, and contains islands; adjoining it are sloughs and backwater areas. The bottom varies from sand to cobble and boulders and is often cemented as outcroppings of upper Ringold-

TABLE 2. C/UE[a] and RAI[b] of numerically dominant species caught by gill net, hoop net and beach seine from June, 1973, through May, 1974, at km 605-613; and October, 1974, through September, 1975, at km 557-566.

| Species | C/UE at km 605-613 | | | | C/UE at km 557-566 | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Gill Net | Hoop Net | Beach Seine | RAI | Gill Net | Hoop Net | Beach Seine | RAI | |
| *Ptychocheilus oregonensis* | 2.79 | 0.48 | 2.98 | 2.08 | 2.13 | 0.28 | 0.78 | 1.06 | (4)[c] |
| *Richardsonius balteatus* | 0.24 | 0.99 | 4.64 | 1.96 | 0.84 | 0.17 | 0.62 | 0.54 | (7) |
| *Catostomus macrocheilus* | 0.64 | 0.15 | 2.82[d] | 1.20 | 2.84 | 0.23 | 1.06[d] | 1.37 | (2) |
| *Oncorhynchus tshawytscha* | 0.30 | 0.01 | 2.54 | 0.95 | 0.09 | 0.02 | 17.01 | 5.71 | (1) |
| *Mylocheilus caurinus* | 0.49 | 0.01 | 0.22 | 0.24 | 1.70 | 0.01 | 1.59 | 1.10 | (3) |
| *Acrocheilus alutaceus* | 0.49 | 0.01 | 0.01 | 0.17 | 2.23 | 0.03 | 0.01 | 0.76 | (5) |
| *Prosopium williamsoni* | 0.51 | | 0.01 | 0.17 | 0.34 | | 1.84 | 0.73 | (6) |
| *Salmo gairdneri* | 0.19 | | | 0.06 | 0.50 | 0.02 | | 0.17 | (8) |
| *Acipenser transmontanus* | 0.19 | | | 0.06 | 0.29 | | | 0.10 | (10) |
| *Cyprinus carpio* | 0.15 | | | 0.05 | 0.27 | 0.01 | | 0.09 | (11) |
| *Gasterosteus aculeatus* | | 0.12 | 0.02 | 0.05 | | | | | |
| *Catostomus columbianus* | 0.12 | 0.01 | | 0.04 | 2.17 | 0.08 | 0.03 | 0.76 | (5) |
| *Perca flavescens* | | 0.01 | | | 0.39 | 0.08 | 0.01 | 0.16 | (9) |
| *Rhinicthys cataractae* | | | 0.01 | | | 0.01 | 0.29[e] | 0.10 | (10) |
| *Ictalurus punctatus* | | | | | 0.20 | 0.01 | | 0.07 | (12) |
| *Pomoxis nigromaculatus* | | | | | 0.09 | 0.04 | | 0.04 | (13) |

[a] Catch per Unit Effort.
[b] Relative Abundance Index.
[c] Numerical Rank.
[d] Includes some juvenile *Catostomus* sp.
[e] Includes some juvenile *Rhinicthys* sp.

type material (Page, Wolf, Gray, and Schneider, 1974). Additionally, the downriver area is under the influence of the upper end of McNary Dam pool and the free-flowing Columbia River above. Both lotic and lentic habitats, as well as wider temperature ranges, are available. Thus, the downriver area has a greater habitat diversity than the upriver collecting sites.

Other species known to inhabit the Hanford Reach of the Columbia River (Table 1) are documented in fish collections at Battelle, Pacific Northwest Laboratories. These include white crappie *(Pomoxis annularis),* tench *(Tinca tinca),* burbot *(Lota lota),* river lamprey *(Lampetra ayresi),* lake whitefish *(Coregonus clupeaformis),* and cutthroat trout *(Salmo clarki).* Cutthroat trout were collected before construction of McNary Dam but not since (Watson, personal communication).

Several other species collected from Columbia River backwater areas south of Richland or occasionally caught by sport fishermen and known to inhabit the lower Snake and Yakima Rivers may be present. These include mosquito fish *(Gambusia affinis),* blue catfish *(Ictalurus furcatus),* nine spine stickleback *(Pungitius pungitius),* and western brook lamprey *(Lampetra richardsoni)* (Becker and Watson, personal communication).

To our knowledge this is the first complete fish species list ever published for the Hanford Reach of the Columbia River, now an environmental research park, and should be of value for ichthyologists in future nuclear power plant siting considerations.

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# First Specimen of Rosethorn Rockfish, Sebastes helvomaculatus (Ayres 1859), Recorded from Puget Sound, Washington

**Abstract**

In Puget Sound, Washington, the rockfish family (Scorpaenidae) is one of the largest in terms of speciation. Twenty-one species (DeLacy *et al.,* 1972) have been reported to date. The fish described below adds another to the total.

On September 12, 1975, a specimen identified as a rosethorn rockfish, *Sebastes helvomaculatus,* was collected during a National Marine Fisheries Service survey of recreational fishery resources off Bainbridge Island, Washington. The specimen, a 297 mm long (total length) female, was caught on an artificial blue-rubber worm in 75 m of water in central Puget Sound (Lat 47°42′N, Long 122°30′W).

A number of specimens identified as *S. helvomaculatus* have been reported from the coasts of Oregon, Washington, British Columbia, and Alaska by Heyamoto and Hitz (1962), Alverson *et al.* (1964), and Westrheim (1965), but none have been recorded from Puget Sound (DeLacy *et al.,* 1972).

Le-Chai Chen (1971) and Westrheim (1965) mention the problems involved in identification of this species of rockfish. Both authors note that similarities between *S. helvomaculatus* and *S. rosaceus* have often resulted in misidentification. Westrheim (1965) comments that a specimen of *S. rosaceus* reported by Clemens and Wilbey (1961) has since been found to be *S. helvomaculatus.* Hart (1973) notes that *S. rosaceus* has subsequently been removed from the Canadian checklist. Chen describes the range of the *S. rosaceus* as being from Turtle Bay, Baja, California, northward to at least San Francisco and the range of *S. helvomaculatus* as being from Albatross Bank, Gulf of Alaska, to Coronado Bank off San Diego, California. Chen also comments

TABLE 1. Comparisons of rosethorn rockfish and rosy rockfish.

| Feature | Rosethorn, *S. helvomaculatus* | Rosy, *S. rosaceus* |
|---|---|---|
| Geographic range | Coronado Bank to Albatross Bank | Turtle Bay, Baja, to San Francisco Bay |
| Body color | Orange yellow with olive-green mottling on back | Orange red, white ventrally; wide purple band across nape |
| Dorsal rays | XIII, 13 (12-14) | XIII, 13 (11-14) |
| Anal rays | III, 6 (6-7) | III, 6 (5-7) |
| Pectoral rays | 16 (15-17) | 17 (16-18) |
| Rakers—1st arch | 28-33 (8-11 + 20-23) | 29-34 (8-11 + 20-24) |
| Pores—lateral line | 35-45 | 37-46 |
| Cranial ridges and spines | Very high and sharp | Relatively weak |
| Concavity of interorbital space | Strong | Moderate |

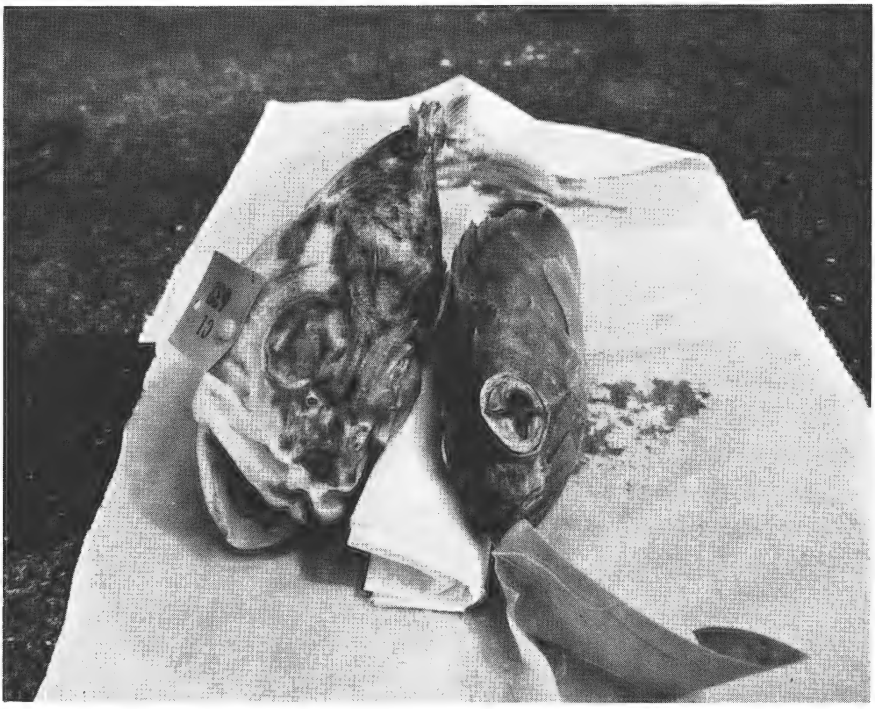

Figure 1. *S. helvomaculatus* (left) and *S. rosaceus* (right). Differences in cranial ridges and spines, and of interorbital concavity are made more apparent with this visual comparison. (Photo by P. Washington.)

that records of *S. rosaceus* from Washington waters (Rathbun, 1894; Evermann and Goldsborough, 190'; Hubbs, 1928; and Schultz, 1936) are questionable in that the specimens were most likely misidentified and probably were *S. helvomaculatus.* Some of the above rockfish were caught in Puget Sound; these were taken by Evermann and Goldsborough (1906) off Morrowstone Point. From their comments in the text, it is apparent that Evermann and Goldsborough questioned the identification of these rockfish to species.

Table 1 lists the features of *S. helvomaculatus* and *S. rosaceus* which were considered during the identification of the specimen taken on September 12, 1975. With the exception of body color of *S. helvomaculatus,* all of the listed information in the table is from Chen (1971); body color of *S. helvomaculatus* follows the description of Phillips (1957).

A description of the specimen taken on September 12, 1975, is as follows: Dorsal XIII, 13; Anal III, 7; Pectoral 16; Rakers on first gill arch 28 (8+20). The interorbital space is strongly concave, and the elevation of the cranial ridges and spines is quite pronounced. Nuchal and coronal spines were absent. The peritoneum is grayish

with fine black dots. The body coloration in life was a bright orange with olive-green spots on the upper body and top of head. Four white to pink spots were present on the upper part of the body and light purple could be seen at the base of the fins. The fish was deposited in Seattle at the museum of the University of Washington College of Fisheries and given catalogue number 20621/group No. 53.

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# Impacts of Impoundment to Vertebrate Animals and Their Habitats in the Snake River Canyon, Washington

## Abstract

Impoundment by Lower Granite Dam on the Snake River in southeast Washington inundated 1,319 ha (3,260 a) of wildlife habitat; 210 ha (620 a, 16 percent) represented tree-shrub riparian habitat and 1,109 ha (2,740 a, 84 percent) represented weedy-floodplain habitat. These habitats were of paramount importance to wildlife at all seasons, but particularly in winter. Sixty-five (50 percent) of 129 species studied were found to be significantly dependent upon tree-shrub riparian habitat. Thirty-four (26 percent) of the 129 species were significantly dependent upon riverbank-floodplain habitat.

Evidence obtained by this study indicates that birds forced from these habitats by inundation will not be able to re-establish themselves in remaining above-pool habitats which were filled to capacity before impoundment occurred. Furthermore, the loss of below-pool habitats will indirectly cause a decrease in the number of birds remaining in above-pool habitats. The greater a species' dependence on tree-shrub riparian or riverbank-floodplain habitat, the greater the impact of impoundment on that species.

Impoundment is estimated to cause a loss locally of nearly 14,000 birds in summer and over 30,000 birds in winter; both estimates are conservative. Migrant birds (excluding waterfowl) did not utilize the lower Snake River Canyon habitats to a great degree, and thus will not be affected nearly as much as permanent, summer, and winter residents.

Since vertebrate species on the Lower Granite area will be affected differentially by habitat loss, population density of these species will decline disproportionately. Some species will be forced completely from the area. All upland game birds will decrease after impoundment; Ring-necked Pheasants will be reduced the most because of this species' strong dependence upon the floodplain. Although Chukar partridge populations declined 46 percent from 1972 to 1973, this upland game bird will very probably maintain relatively high population densities in future years. The overall impact to vertebrates will be a high loss in individual numbers and a decrease in their diversity.

Opportunities for management in the area of Lower Granite Reservoir are very limited. The most productive soils that were washed down to the river from the canyon slopes are now inundated, and only shallow rocky soils extend above pool level. These shallow soils will not support high quality riparian and floodplain habitats, thus resulting in a permanently reduced and simplified vertebrate fauna.

## Introduction

As the present cost for supplying energy to an ever-increasing population accelerates throughout the world, the northwest region of the United States appears to be in the enviable position of having a vast and ready energy source. Currently, this region gets 96 percent of its energy (Gulick, 1972) from large, multi-purpose dams constructed primarily on the Columbia and Snake rivers. Although the cost of hydroelectric energy from these dams may seem relatively inexpensive, there is a growing realization that much has been sacrificed in terms of natural habitat, wildlife, sport and commercial fisheries, hunting, and esthetic enjoyment of free-flowing rivers. Idaho Governor Cecil Andrus (1975), in his dedication of Lower Granite Lock and Dam, told the Army

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Corps of Engineers and Congress that "Before I accept this structure, I want to point out that the costs of this system have been horrendous, both in dollars and in costs to our natural resources."

In 1934, the Fish and Wildlife Coordination Act was adopted in an attempt to get contractors to consult the U.S. Fish and Wildlife Service concerning wildlife destruction before starting construction of locks, dams, roads, and translocations. This act was not effective, and thus amendments were added in 1946 and 1958. The present Fish and Wildlife Coordination Act is much stronger and states that ". . . where losses and damages to the wildlife resources occur, the developer must assume the costs of mitigation, operation, and maintenance of separately provided facilities for wildlife, or else the Federal permit to proceed with construction would not be granted" (Mowrey, 1972, p. 15). Now, impact studies must be conducted on areas to be developed, and equitable compensation must be made to the appropriate state for all wildlife lost by development of the proposed project.

Most impact studies involve losses of game animals because their losses can easily be converted to a monetary figure (mainly by estimating the number of man-hours spent hunting). This procedure is not the case with non-game animals; thus, few studies include these species. For two reasons this omission is unfortunate: (1) both game and non-game species are important in an ecosystem; and (2) non-game wildlife is being utilized more and more by photographers, hikers, campers, and other non-consumptive users. Walcheck (1970) made the only known study that included most of the non-game species (of birds) on an area proposed for impoundment. He found species diversity and density greatest in riparian plant communities. Carothers, Johnson, and Aitchison (1974) studied population structure of riparian birds in the Southwest, but their study was not in response to future impoundment.

Numerous impoundment-related studies have been made on the Columbia River. Claire, Scott, and Sanford (1971), working for the Oregon State Wildlife Commission, studied the potential impact of water fluctuations on wildlife above and below Bonneville Dam. They concluded that fluctuating water levels, particularly during a breeding season, would severely reduce waterfowl productivity. The effect on wading birds, shore birds, and hawks was predicted to be minimal; other non-game species were not studied. Oliver and Barnett (1966), from the Washington State Department of Game, estimated the effect that impoundment behind Wells Dam would have on upland game bird populations and concluded that California Quail *(Lophortyx californicus)* and Ring-necked Pheasant *(Phasianus colchicus)* populations would be greatly diminished. Quick and Powell (1961) predicted the same results in a pre-impoundment study on John Day Reservoir. Eicher (1968) found a change in species percentages of waterfowl from pre- and post-impoundment counts on Wells reservoir. He noted an increase in "game" ducks, particularly dabblers, in the post-impoundment study, thus suggesting a beneficial effect (as far as hunters are concerned) from construction of these impoundments. Both Haynes (1970) and Edwards (1975) reported changes in species composition of invertebrates when rivers became impounded. This development, as well as a change in aquatic vegetation, was the probable cause for changes observed in waterfowl species composition by Eicher (1968).

Numerous impoundment-related studies on waterfowl have been done on and near the Snake River. Yocom (1949, 1951) surveyed waterfowl and studied foods eaten by them in eastern Washington; his investigation included the Snake River

Canyon. Johnsgard and Buss (1956) studied waterfowl sex ratios in the Snake River Canyon, and Johnson (1961) studied the reproductive cycle of the Mallard *(Anas platyrhynchos)* in the Snake River Canyon and adjacent uplands. Buss and Wing (1966) conducted a pre-impoundment study of wintering Mallards and breeding Canada Geese *(Branta canadensis)* in the Snake River Canyon. Culbertson (1967) and Culbertson, Cadwell, and Buss (1971) provided information on Canada Geese nesting behavior in the Snake River Canyon and on Little Goose Reservoir. Gibson and Buss (1972) made a study during and after impoundment on Lower Granite and Little Goose reservoirs and found that nesting by Canada Geese was greatly reduced after impoundment. This reduction was attributed to inundation of islands and shore lands previously used by geese for nesting. Hanson and Eberhardt (1971) studied Canada Goose populations on the Lower Snake and Columbia rivers from 1950 to 1970.

Impoundment-related studies on wildlife other than waterfowl have also been conducted on and near the Snake River. Dice (1916) studied distribution of land vertebrates in Walla Walla and Columbia counties and attempted to associate vertebrates with particular habitat types. He noted little riparian vegetation along the Snake River in these two counties, so he did not include it as a habitat type. Dice (1918) continued his bird studies in Walla Walla and Columbia counties and discussed preferred habitats as well as some foraging observations. Dumas (1950) conducted a breeding bird survey of several habitat types in southeastern Washington, finding avian density highest in the floodplain forest (riparian) habitat of the Snake, Walla Walla, Touchet, and Tucannon rivers. Oliver (1968), from studies on Ice Harbor and Lower Monumental reservoirs, predicted losses of gallinaceous birds from hunter-harvest data to be 56-80 percent for all four impoundments. Mackie and Buechner (1963) investigated the reproductive cycle of the Chukar *(Alectoris chukar)* in tributary canyons of the Snake River. Anthony (1970a, b) studied ecology and reproduction as well as food habits of California Quail in the Snake River lowlands, its tributaries, and the wheatlands above the canyon. Morton (1966) made observations of foraging White-crowned Sparrows *(Zonotrichia leucophrys)* between Wawawai Canyon and Clarkston in the Snake River Canyon. Although another White-crowned Sparrow study is in progress, these are the only two studies conducted on passerines in the Lower Granite-Little Goose areas.

An impoundment-related project was conducted in Grant County, central Washington, by Johnsgard (1955). There he investigated nesting and production of waterfowl in relation to water level fluctuations and vegetational change among potholes behind O'Sullivan Dam.

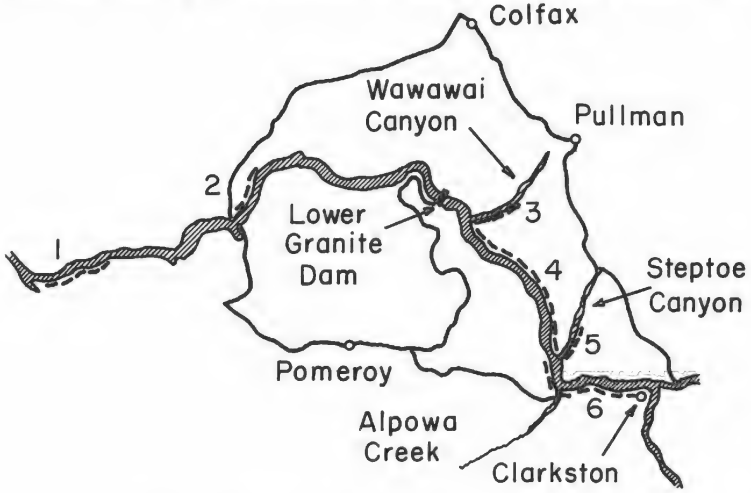
Several reports related to impacts of the Snake River impoundments have been produced recently. Impact reports of Ice Harbor, Lower Monumental, and Little Goose dam projects were prepared by the U.S. Department of Interior for the Army Corps of Engineers in two reports (1972, 1973). These reports recommended mitigation for fish and wildlife losses, but, for the most part, ignored non-game wildlife. A study conducted by Buss (1975) for Wirth Associates and the Army Corps of Engineers provides an inventory of corps-owned wildlife lands which border the four reservoirs of the Lower Snake River Project. Consideration for non-game wildlife, particularly rare and endangered species, is included in the study. Finally, the U.S. Army Corps of Engineers in 1973 funded three universities (University of Idaho, Oregon State University, and University of Washington) for an inventory of riparian habitats and

associated wildlife along the Columbia and Snake rivers. This study will include reptiles, amphibians, birds (game and non-game), mammals (game and non-game), and plants.

Lower Granite Dam was the last dam constructed on the Lower Snake River. The reservoir behind this dam was filled in February, 1975. The creation of this reservoir inundated nearly all riverbank and floodplain habitats, causing a drastic loss of important riparian vegetation. In the spring of 1972, the present study was initiated with the following objectives: (1) to quantify effects of Lower Granite Reservoir on certain game and non-game animal populations; (2) to study utilization of riparian,[1] weedy floodplain, and other habitat types in part of the Snake River Canyon adjoining Lower Granite Reservoir; and (3) to provide information on foraging strategies of avian species utilizing various terrestrial habitats bordering Lower Granite Reservoir. Results for the third objective will be presented in a later paper.

**Description of Study Areas**

The Lower Snake River Canyon extends about 225 km (140 mi) from its mouth at the Columbia River to Clarkston in southeastern Washington and presently includes all of Ice Harbor, Lower Monumental, Little Goose, and Lower Granite reservoirs to Clarkston (see Fig. 1 for location of landmarks and study areas). The canyon was




Study Areas for Road Counts

1. Lower Monumental } combined as LGLM or
2. Little Goose } Little Goose - Lower Monumental
3. Wawawai Canyon
4. Lower Granite - North Side
5. Steptoe Canyon
6. Lower Granite - South Side

Figure 1. Location map of study areas.

[1] Hereafter refers only to tree-shrub riparian vegetation.

scoured out of a basalt plateau that tilts from about 762 m (2,500 ft) above mean sea level (msl) at the Washington-Idaho boundary to about 122 m (400 ft) above msl near the mouth of the Snake River (U.S.D.I. Geological Survey, 1973). Consequently, height and steepness of canyon slopes decrease progressively as one proceeds westward. This gradient in elevation has an important influence on climatic conditions in the canyon. As the prevailing westerly winds move air masses up the gradually rising plateau, precipitation slowly increases, reaching an annual total of at least 51 cm (20 in) near the Washington-Idaho boundary. Thus, there are more trees and shrubs on the main canyon slopes and tributary canyons of the Lower Granite Study Area than those of Little Goose or Lower Monumental reservoirs where grasses and herbs are dominant.

Before impoundment, the river moved at about 6 km (4 mi) per hour, and there were only a few rapids, all easily navigable. After the reservoirs in the Lower Snake River Canyon were filled, very little riparian vegetation remained. Floodplains are still present and tend to be large in places such as those near the confluence of the Palouse and Tucannon rivers with Lower Monumental Reservoir. Floodplain soil is a combination of silt wash from the surrounding plateaus, glacial gravel and sand, and river sand of granitic origin (Weaver, 1917; Fenneman, 1931). Large sand bars (Fig. 2), supporting *Salix* spp., *Glycyrrhiza lepidota, Xanthium strumarium,* and other plants which were an important component of Canada Goose habitat (Buss and Wing, 1966; Culbertson *et al.,* 1971), were abundant before impoundment, particularly in the Lower Granite Study Area.

The lower Snake River canyon is a very dry, warm region in the summer with temperatures averaging 23° C for June, July, and August (Phillips, 1970). Winter temperatures (December-February) generally are mild (mean = 20° C), and readings below –18° C are infrequent (Phillips, 1970). Annual precipitation is 27 cm, most of it (78 percent) coming in late fall, winter, and early spring (October to April) (Phillips, 1970). Relative humidity in summer (1600) is low (28 percent), but rises much higher (70 percent) in winter or rainy seasons (Phillips, 1970). Average snowfall is 21 cm annually (Phillips, 1970). Wind velocity can be high, but rarely over 40 km/hr (25 mph) because the prevailing westerly winds are funneled up the canyon. North-facing slopes receive less direct sunlight than the south and consequently have a cooler and more moist micro-climate. Monthly climatological data for the area are available from U.S. Weather Bureau and U.S. Environmental Data Services publications.

*Lower Granite Study Area*

The major part of this study was conducted in the upper 63 km (39.1 mi) of the Lower Snake River Canyon between Asotin and Lower Granite Dam; in this report, the area is referred to as the Lower Granite Study Area. Since this study was initiated in the spring of 1972, and Lower Granite Reservoir was impounded in February, 1975, nearly three years were available for obtaining pre-impoundment observations of vertebrate animals and their habitats on this last stretch of free-flowing river in the Lower Snake River Canyon. Field work was conducted on canyon slopes, in tributary canyons, and on floodplains and banks of the free-flowing Snake River.

Canyon slopes generally are steep, with basalt bluffs rising 2,000 ft to the rolling uplands of wheat and pea fields. Many small creeks in wooded tributary canyons enter the main canyon. Prior to impoundment, many of these tributary streams formed

Figure 2. Typical sandbar in Lower Granite Study Area with *Glycyrrhiza lepidota* in the foreground and *Salix* sp. in the background.

large alluvial fans. Alpowa Creek, 13 km (8 mi) downstream from Clarkston, is the largest tributary in this 63 km (39.1 mi) segment of the canyons. State and county roads extended along the entire north bank and for 13 km (8 mi) downstream from

Figure 3. Aerial photograph of the Alpowa Creek Study Area.

Clarkston along the south bank.

Daubenmire (1970) includes the entire study area within the *Agropyron spicatum-Poa secunda* vegetation zone. Because of the substantial overgrazing by cattle, little of the original vegetation remains except in the more inaccessible sites. Within this zone, stands representing several different vegetation types can be identified. On lithosols of the basaltic slopes, *Eriogonum niveum, Artemisia rigida,* and *Poa secunda* are most common. In deeper soils on slopes and along railroad tracks some *Agropyron spicatum* remains. *Rhus glabra* and *Chrysothamnus nauseosus* often extend from the floodplains to variable distances up the slope (see Fig. 4). Draws are dominated by trees and shrubs with *Rosa* sp., *Rhus glabra, Rhus radicans, Rubus* sp., and *Sambucus glauca,* the most common shrubs, and *Celtis reticulata* and *Alnus rhombifolia,* the most abundant tree species (see Fig. 5). *Symphoricarpos albus* is more common in cooler and more moist north-facing draws than in the drier south-facing draws (Anthony, 1970a).

Floodplains and alluvial fans frequently supported stands of *Celtis reticulata* with *Chrysothamnus nauseosus* and *Opuntia polyacantha* abundant in various sites. *Bromus tectorum* is the dominant grass; forbs such as *Salsola kali, Helianthus annuus, Sisym-*

Figure 4. Riparian woodland along the river bank with bunch grass *(Agropyron spicatum)* on the steep bank above the railroad tracks in Lower Granite Study Area.

*brium altissimum,* and *Centaurea solstitialis* are very common. All fruit orchards had been removed by 1972 when this project was initiated.

River bank vegetation often consisted of a thick tangle of trees and shrubs (see Fig. 6). *Salix* sp., *Morus alba,* and in some places *Celtis reticulata* were the dominant tree species; the shrubs *Rosa* sp., *Rhus glabra, Rhus radicans,* and *Ribes aureum* were very abundant in many places. Herbaceous understories usually contained *Bromus tectorum* along with *Urtica dioica, Conium maculatum,* and various thistles *(Cirsium* spp., and *Onopordum acanthium*). Shoreline vegetation consisted of small willows, various species of *Polygonum,* and *Iva axillaris.* Sandbars nearly always contained *Xanthium strumarium.* See Wakefield (1966), Buss and Wing (1966), Clegg (1973), and Lewke (1975) for a more detailed description of the vegetation of the Lower Granite and Alpowa Creek Study Area.

*Alpowa Creek Study Area*

This study area is located on the south bank of Lower Granite Study Area, 13 km (8 mi) west of Clarkston, adjacent to U.S. Highway 12, near the mouth of Alpowa Creek

Figure 5. Ravine on the south side of the river showing riverbank-floodplain and draw-cliff topographic types.

(see Figs. 1 and 3). A large, lush stand of riparian vegetation occurred here prior to impoundment (Fig. 4). The photograph for Figure 3 was taken before this study began and before the orchards seen in the photograph were removed. Eleven ha (28 a) were sampled to obtain population density estimates of birds utilizing riparian and weedy-floodplain habitats. Elevation is from 210 to 223 m (690 to 730 ft) above msl. Since the pool level is 225 m (738 ft) above msl, the entire Alpowa Creek floodplain is now under water. Alpowa Creek had one of the largest floodplains upstream from Lower Granite Dam.

*Little Goose and Lower Monumental Study Area*

Relatively little time was devoted to field work on Little Goose and Lower Monumental reservoirs, which are located consecutively downstream from Lower Granite Dam. Little Goose Reservoir is about 68 km (42 mi) in length, whereas Lower Monumental, the smallest reservoir in the Lower Snake River Canyon, is only about 48 km (30 mi) in length. As noted above, height and steepness of canyon slopes decrease progressively as one traverses the reservoirs from east to west, and there is conspicuously less woody vegetation than in Lower Granite Study Area.

A major difference between Little Goose post-impoundment study area and the Lower Granite Study Area is the almost total absence of riparian vegetation. The small section studied had little riparian vegetation; so, too, an aerial reconnaissance revealed very little along the entire reservoir. Small willow shrubs are scattered in places along the shore. More commonly, *Bromus tectorum* extends down to a rocky or sandy shore.

Floodplains, even after impoundment, are more extensive along Little Goose Reservoir than in the Lower Granite Study Area. *Bromus tectorum* and *Sisymbrium altissimum* dominate, with *Helianthus annuus* abundant in the summer. The upper part of

Figure 6. Riparian woodland at the Alpowa Creek Study Area dominated by *Salix* sp., *Morus alba,* and *Ribes aureum.*

a floodplain contains *Chrysothamnus nauseosus* and *Eriogonum niveum* in abundance. Most of the trees present are at an abandoned farm and a Washington State University agricultural station. *Robinia pseudoacacia* is the most abundant tree; there are a few *Morus alba* and *Salix* sp. present.

Draws are shallow and for the most part devoid of trees and shrubs, with ground cover dominated by *Bromus tectorum.* Slopes are accessible to cattle, and have been extensively overgrazed. *Chrysothamnus nauseosus* and *Bromus tectorum* dominate, with *Agropyron spicatum* remaining in a few sites.

Post-impoundment shoreline vegetation for much of the section studied along Lower Monumental is almost nonexistent because of rock abutments for roads. In other sections, vegetation is similar to that in Little Goose Reservoir. Thick riparian vegetation is scarce.

Floodplains are dominated by *Bromus tectorum* and *Sisymbrium altissimum; Chrysothamnus nauseosus* and *Eriogonum niveum* are dominant in the upper part of floodplains. *Lactuca serriola* and *Helianthus annuus* are common in summer and fall. At the base of the steep slopes are scattered patches of *Clematis ligusticifolia, Rosa woodsii,* and *Ribes aureum.*

Draws are similar to those in Little Goose Reservoir, but do contain some low *Celtis reticulata, Prunus virginiana, Philadelphus lewisii,* and *Rhus radicans. Bromus tectorum* is abundant as ground cover. Slopes are steep and not as heavily grazed as in Little Goose Reservoir. Good stands of *Agropyron spicatum* and *Poa secunda* remain.

Obviously, the vegetation of Lower Granite Study Area, particularly in draws and along shorelines, is much more abundant and diverse than in the lower two reservoirs. The impoundment caused by Lower Granite Dam has destroyed nearly all riparian vegetation, leaving the reservoir shoreline similar (except for heavily vegetated draws and minimal floodplain acreage) to that of the two lower reservoirs.

### Methods

Three types of data were collected to evaluate the impact of Lower Granite Reservoir on vertebrate species: (1) pre-impoundment indices of relative abundance derived from transect, road count, hunter check stations, and small mammal trapping data; (2) habitat preference data gathered from transect, road count, and Alpowa Creek studies; and (3) avian population estimates (to estimate loss of game and non-game birds from Lower Granite Study Area).

#### *Relative Abundance Indices*

*Transects.* Twenty-four transects perpendicular to the Snake River were established on the north side of Lower Granite Study Area and 20 on the south side in the spring of 1972. A review of these transects during the summer of 1972 resulted in elimination of three transects from the north side and 16 from the south side. As road translocation and construction progressed on the north side, some transect extensions were needed. By spring of 1973, construction work had eliminated all but 16 transects which could be used on the north side. Analysis of four preceding counts showed that 94 percent of all species were observed on these 16 transects; thus, no additional transects were added. Table 1 gives the location of each transect on the north side. South side transect locations were omitted, since they became inaccessible by land after impoundment. Table 2 shows total transect distances walked above and below prospective pool level

TABLE 1. Location of transects on the north side of Lower Granite Study Area.[a]

| Transect No. | Distance (km) |
|---|---|
| 1 | 3.9[b] |
| 2 | 2.6[b] |
| 3 | 1.9[b] |
| 4 | 3.2 |
| 5 | 3.9 |
| 6 | 4.3 |
| 7 | 6.4 |
| 8 | 6.8 |
| 9 | 7.8 |
| 10 | 9.6 |
| 11 | 9.7 |
| 12 | 10.2 |
| 13 | 10.9 |
| 14 | 11.7 |
| 15 | 12.0 |
| 16 | 12.2 |
| 17 | 12.5 |
| 18 | 13.8 |
| 19 | 14.6 |
| 20 | 17.5 |
| 21 | 17.8 |

[a]Distance calculated from junction of Steptoe Canyon road with river road.
[b]Upstream; all others are downstream.

during each season. Transect lengths varied between 210 and 617 m, and all transects but one were in draws. For easy location of transects in the future, numbers were painted on rocks visible from the road.

Teams of four wildlife students from Washington State University started walking the transects at sunrise and continued until all transects assigned to them (2-4 per team) had been walked. Two members walked and recorded vertebrate sightings, while the other two recorded on a transect map the location, size, and type of plant communities crossed by a transect. (Two recorders walking the same 805 m transect represent only 805 m of censused transect.)

For each vertebrate observation within 91 m (100 yd) of the transect, the observation number, species, number of individuals seen, positive or questionable identification, physiognomic and topographic type in which an animal was seen, whether above or below pool level, and plant community in which an animal was seen (optional) were recorded on a data sheet. Observations were numbered consecutively and marked on a map of the transect. Data were then converted to number of observations (vertebrates, birds, Galliformes, deer, and rabbits) per transect-mile walked each season. All destruction to the transect by road building was indicated on the vegetation map of each transect. Teams walked the transects three times each season, except summer. A new map and data sheet were used each time a transect was walked.

From the students' vegetation maps of each transect, the percentage of each physiognomic and topographic type represented on all transects for each season was calculated. These values (and those from the Alpowa Creek Study Area) were used to calculate the number of expected observations (for chi-square analyses) in each physiognomic and topographic type (Table 3).

TABLE 2. Number of transect-kilometers walked each season above and below prospective pool level.[a]

| Year | Side of River | Season | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Spring | | | Summer[b] | | | Fall | | | Winter | | |
| | | Above | Below | Total | Above | Below | Total | Above | Below | Total | Above | Below | Total |
| 1972 | north | 12.9 | 12.4 | 25.3 | . . | . . | . . | 14.0 | 10.8 | 24.8 | 13.5 | 10.3 | 23.8 |
| 1972 | south | 8.8 | 13.8 | 22.6 | . . | . . | . . | . . | . . | . | . . | . . | . . |
| 1973 | north | 10.8 | 8.8 | 19.6 | . . | . . | . . | 11.6 | 8.7 | 20.3 | 11.6 | 8.7 | 20.3 |
| 1973 | south | 2.6 | 2.3 | 4.9 | . . | . . | . . | . . | . . | . | . . | . . | . . |
| Total | | 35.1 | 37.3 | 72.4 | . . | . . | . . | 25.6 | 19.5 | 45.1 | 25.1 | 19.0 | 44.1 |
| % | | 45 | 52 | 100 | 53 | 48 | 101 | 57 | 43 | 100 | 57 | 43 | 100 |

[a]Number of transect-kilometers determined by multiplying each transect length by the number of times the transect was walked (usually three), and then summing over all transects.

[b]Since transects were not studied in summer, percentages for above and below categories are averages of spring and fall percentages for each category.

TABLE 3. Composition (%) of physiognomic and topographic types in Lower Granite Study Area.[a]

| Season | Physiognomic Type | | Topographic Type | | | |
|---|---|---|---|---|---|---|
| | Non-riparian | Riparian | Riverbank | Floodplain | Draw | Cliffs |
| Spring | 67 | 33 | 2 | 55 | 12 | 31 |
| Summer[b] | 68 | 32 | 2 | 53 | 13 | 32 |
| Fall | 69 | 31 | 2 | 51 | 14 | 33 |
| Winter | 69 | 31 | 2 | 51 | 14 | 33 |
| Average[c] | 68 | 32 | 2 | 52 | 13 | 32 |

[a]Physiognomic type percentages are averages of each season's value for transect plots (1972-1973) and for values from Alpowa Creek Study Area. Topographic type percentages are from transect plot studies alone, as the last two categories were not present at Alpowa Creek.

[b]Summer percentages are averages of spring and fall since no transect studies were conducted in this season.

[c]Summer excluded.

Transect study continued for two years, starting in the spring of 1972 and terminating in the winter of 1973. Transects were walked on the following dates:

15 April to 17 May 1972
22-30 October 1972
10-17 December 1972
5-6, 12-13 May 1973
13-14, 20-21 October 1973
8-9, 15-16 December 1973

*Road Counts.* Road counts were initiated shortly after sunrise at the same location on each study area except Lower Granite Study Area, north side, where counts were started alternately each month at Wawawai or Steptoe canyons. A stop was made every 895 m (½ mi) along the census route, but no attempt was made to stop in exactly the same location each month. At each station the observer stood by the car and recorded every vertebrate seen or heard within a 402 m (¼ mi) radius during a 3-minute period (see French, 1970). The only animals counted were those seen on the side of the river being studied. However, ducks, geese, and hawks observed on or over the river were also counted. An attempt was made to count individuals only once.

At each station all species seen were recorded, as well as the number of individuals (sex and age if possible), whether above or below pool level, and the physiognomic and topographic type in which an animal was seen. Species seen between stations but not observed at any stations were noted but not included in the count totals.

Road counts were made between the 12th and 17th of each month. Table 4 summarizes the number of stations, distances traveled, and counts for each site.

Twenty stations were used for comparisons among areas (excluding the two canyons) because no more stations could be added to the road counts along Little Goose and Lower Monumental study areas (hereafter referred to as Little Goose-Lower Monumental Study Area). An analysis of six of the counts from the north side of Lower Granite Study Area showed that 84 percent of all species recorded at 33 stations had been tallied after 20 stations. Thus, 20 stations per count were considered satisfactory for this study. Even though more stations increase the number of species seen, such added counts are irrelevant because only index figures are being compared from area to area and from season to season.

TABLE 4. Road count sites, number of stations, kilometers, and counts.

| Site | km | No. of stations | counts |
|---|---|---|---|
| Lower Granite Study Area, south side | 15.3 | 20 | 11[a] |
| Lower Granite Study Area, north side | 25.7 | 33[b] | 12 |
| Wawawai Canyon | 4.8 | 7 | 12 |
| Steptoe Canyon | 4.8 | 7 | 12 |
| Lower Monumental Reservoir, south side | 9.7 | 13 | 12 |
| Little Goose Reservoir, south side | 4.8 | 7 | 12 |
| U.S. Highway 195 (Colfax highway) | 15.3 | 20 | 2 |

[a]Road relocation prevented the March count from being made.
[b]Only the middle 20 stations were used in comparison with other areas.

Although road counts are biased toward the more conspicuous species, this bias can be ignored because only index values rather than true population estimates were derived. Conspicuousness of each species was assumed to remain constant from year to year.

*Species Diversity Calculation.* Bird species diversity (BSD) indices[2] of Little Goose-Lower Monumental and Lower Granite Study Area were calculated from road count data using the Shannon and Weaver (1949) information content formula

$$H' = p_i \log p_i \qquad (2)$$

where $p_i$ represents the proportion of observations found in the $i^{th}$ category, and H′, for this study, is species diversity. A form of this equation which simplifes the calculation of diversity is:

$$H' = \frac{C}{N} (N \log_{10} N - n_i \log_{10} n_i) \qquad (3)$$

where H′ again is the species diversity index, N is the total number of individuals in all species, $C = 1$ for base ten, and $n_1$ is the number of individuals in the $i^{th}$ species (Lloyd, Zar, and Karr, 1968). These authors also tabulate values of $n \log_{10} n$ for all integers from 1-1,050, which makes computation of H′ relatively easy. Species diversity values generally fall between zero (no diversity) and three (high diversity), although theoretically diversity could approach infinity if the number of species was very large. Diversity is greatest in communities where the individuals are evenly dispersed among all species present. If two communities both have individuals evenly dispersed, the community with the larger number of species will have the larger species diversity. An analysis of variance has been used on indices of Little Goose-Lower Monumental and Lower Granite Study Areas. Significance was tested by an "F" test. In all cases the 5 percent level of significance was used.

*Hunter Check Stations.* In the fall and winter of 1972 and 1973, hunter check stations were located at the first road junction at the top of Steptoe Canyon, at the bottom of Wawawai Canyon, and on the River Road several miles east of its junction with U.S. Highway 195. Two checkers worked at each station from 10 A.M. until dark on both Saturday and Sunday of alternate weekends; the first weekend of checking each

[2]Pielou (1966, p. 131) defines diversity as ". . . the degree of uncertainty attached to the specific identity of any randomly selected individual. The greater the number of species and the more nearly equal their proportions, the greater the uncertainty and hence the diversity."

year was the third weekend of the early Chukar season. Checkers recorded the number of each species of game animal shot, the number of hunters in each party, whether dogs were used, and the time spent hunting. Parties were recorded as either bird hunters or deer hunters. At the end of each day and at the end of the last weekend of checking, the data were summarized.

*Small Mammal Trapping.* Teams of three or four wildlife students were assigned one transect each season except summer. Ten clusters of five traps each (50 Victor mouse-sized snap traps per transect) were placed in different vegetation types encountered along each transect. Students were encouraged to trap in as many different vegetation types as possible, and to divide the clusters evenly between above- and below-pool level sites. The location of each cluster was marked on a transect map along with the vegetation surrounding each cluster. Traps within each cluster were set at a 1.5 m radius from a metal stake marking the cluster location. If cluster sites were destroyed or could not be found the next season, new sites were chosen. Smooth peanut butter was used as bait.

Trap lines were checked at dawn and dusk—approximately 12-hour intervals—for two successive days. Each mammal caught was tagged and returned to the laboratory for positive identification, sex determination, age estimation, and weighing. Length (total, tail, and hind foot) and, if a female were pregnant, the number of embryos were recorded. The cluster number, physiognomic type, vegetation type (optional), pool level, cover value, and soil depth were also recorded. Plant cover for each trap site was classified as follows:

VG = very good (plant cover more than 75 percent of ground surface).
G = good (plant cover over 25-75 percent of ground surface).
F = fair (plant cover over less than 25 percent of ground surface).

Soil depth at each cluster site was obtained by an average of 25 measurements (with a calibrated metal rod) as follows:

S = shallow (10 cm).
M = medium (10-30 cm).
D = deep (30 cm).

Mouse-sized snap-traps were set in the Alpowa Creek Study Area (as described above) along a trap line extending through the following six different habitat types: short and tall weed fields, riparian woodland, willow flat, sage flat, and tall rye grass *(Elymus cinereus).* Traps were checked at dusk and dawn for three successive days and nights (7-10 June 1973). All data except weight and length were recorded as described previously.

Three wildlife students snap-trapped the same lines in late winter (28 February to 3 March 1974) in the same manner to see if small mammal distribution in winter was different from that found in summer. Two different teams of four students each live-trapped (Sherman live-traps) and can-trapped similar lines on the Alpowa Creek study site to compare the effectiveness of two trapping techniques. Since some animals, particularly shrews (Brown, 1967), are snap-trap shy, all three trapping techniques were used to increase the probability of capturing most or all small mammal species present. Cans used were 15 cm (6 in) in diameter and 18 cm (7 in) deep. Each was half-filled with water and sunk with the rim flush with the ground surface. Ten clusters of five cans each were located in a variety of plant communities. Cans within each

cluster were placed at a radius of 3 m (10 ft). Fifty-eight live traps were set in groups of two at 9-m (10-yd) intervals in several different vegetation types.

*Habitat Preference*

To reveal habitat preference, every sighting of a vertebrate while conducting transect walks or road counts was recorded in one of the following physiognomic types: 1) Lichens, Mosses, and Bare Rock; 2) Bunchgrass Dominant *(Agropyron)*; 3) Short Grass Dominant *(Bromus, Poa)*; 4) Tall Herb Dominant; 5) Sagebrush Dominant *(Artemisia rigida* and *A. tripartita);* 6) Rabbit Brush Dominant *(Chrysothammus);* 7) Open Shrub *(Rhus* or low *Celtis)*; 8) Closed Shrub *(Amelanchier, Rubus, Philadelphus,* etc.); 9) Tree (savanna type appearance); and 10) Tree-Shrub. For this report the above categories were lumped into two major physiognomic types: riparian (includes types 7-10) and non-riparian (includes types 1-6).

Because the same physiognomic type can occur in different locations, one of the following topographic types was recorded for each vertebrate sighting: A) River Bank, B) Upper River Bank, C) Floodplain, D) Draw, and E) Rocky Slopes and Cliffs. River bank and upper river bank types later were combined. Finally, each vertebrate sighting was recorded as occurring above or below projected pool level.

*Avian Population Estimates for Lower Granite Study Area*

Avian population densities were estimated for riparian and non-riparian floodplain habitats for the entire Lower Granite Study Area from comprehensive censuses at the Alpowa Creek Study Area. Errors can occur when extrapolating from small to large areas, but in lieu of counting all birds in the valley between Lower Granite Dam and Asotin, Washington—which is physically impossible—one is left with no other alternative. High and low estimates presumably tend to balance each other.

The area of riparian and non-riparian habitats at Alpowa Creek and 22 km (13.7 mi, 35 percent) of Lower Granite Study Area was estimated by using 36 dots per 645 sq. mm (1 sq. in) plastic grid and aerial photographs (series W72-2, 3, and 4) supplied by the Corps of Engineers, Walla Walla, Washington. The following formula from Avery (1968) was used:

$$\frac{(\text{map scale})^2 \div}{6{,}272{,}640} 36 = \text{acres per dot } (\div 2.471 = \text{ha})$$

Total area for various habitats along Lower Granite Reservoir was obtained by extrapolating from the values found from the examination of both sides for 22 km (13.7 mi) of river. Total distance for the reservoir between Asotin and Lower Granite Dam is 63 km (39.1 mi).

Estimates of floodplain area were made with the 36 dots per 645 sq. mm grid and reservoir maps (Design Memorandum No. 3, File No. GD-05-4/33-45) supplied by the Corps of Engineers at Walla Walla.

Two methods of censusing bird populations were used: the singing male technique (see Kendeigh, 1948; Williamson, 1964; and Snow, 1966) for most summer breeding birds, and sight location for non-singing summer birds and all winter birds. Locations of all observations were recorded on a map of each habitat and later tabulated. In late spring through summer, five censuses were conducted; eight were made in winter (Kendeigh [1944] recommends at least five). The maximum count recorded during each season for each species was used as the population estimate for that species in

that particular habitat. Results obtained by the singing male technique were doubled to account for females. Errors caused by non-mated males singing are assumed to be balanced by missing some males which were not singing. Results are expressed as number of birds per 41 ha (100 a), as recommended by Lack (1937).

Botanical nomenclature is from Hitchcock and Cronquist (1973), and avian nomenclature follows the A.O.U. Checklist (1957) and Supplement (1973).

## Results

### *Pre-impoundment Index Information*

*Transect Data.* Vertebrate sightings along transects in Lower Granite Study Area are presented in Table 5. The total number of vertebrates per 1.6 km transect (1 mi) was highest (157.5) during spring, 1973, on the south side of the area and lowest (35.6) during fall, 1973, on the north side (Table 5). Most of the vertebrates observed were birds, which comprised at least 78 percent (Spring, North side, 1972) of the total number of species recorded for any year, season, or transect site (Table 5).

The preponderance of bird sightings is reflected in the high similarity between number of vertebrates per 1.6 km transect (1 mi) and number of birds per 1.6 km transect shown during both years, all seasons, and on all transect sites in Table 5.

The number of birds observed per 1.6 km transect from 1972 to 1973 on the north side of Lower Granite Study Area is presented in Figure 17 for comparative purposes (see p. 258).

Lewke (1975) presents abundance and frequency data for each bird species observed on the transect counts.

*Road Counts and Species Diversity Data.* Table 6 gives results from road counts conducted each season in Lower Granite Study Area south side, Lower Granite Study Area north side, and Little Goose-Lower Monumental Study Area, respectively. Index data from road counts give better coverage of all habitats in the valley than index data from transects which provide information primarily from vertebrates occupying draws.

The average number of bird species and individual counts per season are included in Table 6 so that comparisons can be made among study areas. Information obtained on abundance and frequency of each bird species observed is presented by Lewke (1975).

To visualize more easily the magnitude of diversity in these Snake River study areas, two road counts were conducted (one in June and the other in December) along 15 km (9.5 mi, 20 stations) of U.S. Highway 195 surrounded by agricultural land (Lewke, 1975). These results were then compared to those from the Snake River study areas.

Figures 7-9 summarize the results presented in Table 6. The south side of Lower Granite Study Area contained more species per road count each season (Fig. 7), more individuals per road count in the spring, summer, and fall (Fig. 8), and a greater species diversity index (Fig. 9) each season than either of the other three study areas. Counts from U.S. Highway 195 were lowest in every category.

As mentioned above, each road count along the north side of lower Granite Study Area had 33 stations, but only the middle 20 were included in Table 6 for comparisons with other areas. The results of each entire road count (33 stations) are available for comparisons with post-impoundment road counts that may be made (Lewke, 1975).

Data on seasonal differences in bird abundance and diversity for three different study areas are presented in Table 6 and illustrated in Figures 7-9. Table 7 shows the

TABLE 5. Vertebrate sightings on transects in Lower Granite Study Area.

| Season | Indices | 1972, North side | | | 1973, North side | | | 1972, South side | | | 1973, South side[a] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Above pool | Below pool | Total | Above pool | Below pool | Total | Above pool | Below pool | Total | Above pool | Below pool | Total |
| Spring | No. of Vert. Species | . . | . . | 45 | . . | . . | 52 | . . | . . | 44 | . . | . . | 36 |
| | No. of Bird Species | . . | . . | 35 | . . | . . | 45 | . . | . . | 40 | . . | . . | 35 |
| | Vert/transect unit[b] | 38.6 | 44.9 | 57.4 | 52.5 | 39.3 | 52.9 | 31.1 | 82.2 | 87.5 | 157.5 | 80.7 | 126.3 |
| | Birds/transect unit | 37.8 | 43.0 | 55.5 | 51.0 | 37.8 | 51.5 | 30.9 | 81.6 | 87.0 | 157.5 | 80.0 | 126.0 |
| | Galliformes/tr unit | 8.1 | 5.3 | 6.9 | 9.9 | 3.1 | 6.8 | 6.4 | 14.3 | 11.6 | 30.0 | 0.0 | 16.0 |
| | Cal. Quail/tr unit | 0.1 | 2.3 | 1.3 | 0.2 | 0.9 | 0.5 | 0.7 | 4.2 | 2.8 | 2.5 | 0.0 | 1.3 |
| | Chukar/tr unit | 7.1 | 2.5 | 4.8 | 8.4 | 0.6 | 4.8 | 4.6 | 7.4 | 6.3 | 26.9 | 0.0 | 14.3 |
| | Gray Part./tr unit | 0.0 | 0.0 | 0.0 | 0.5 | 0.7 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Pheasant/tr unit | 0.9 | 0.5 | 0.8 | 0.9 | 0.9 | 0.9 | 1.1 | 1.7 | 1.6 | 0.6 | 0.0 | 0.3 |
| | Rabbits/tr unit | 0.3 | 1.4 | 1.0 | 0.5 | 0.4 | 0.4 | 0.0 | 0.4 | 0.2 | 0.0 | 0.7 | 0.3 |
| | Deer/tr unit | 0.1 | 0.1 | 0.1 | 0.3 | 0.2 | 0.3 | 0.2 | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 |
| Fall | No. of Vert. Species | . . | . . | 40 | . . | . . | 33 | . . | . . | . . | . . | . . | . . |
| | No. of Bird Species | . . | . . | 36 | . . | . . | 29 | . . | . . | . . | . . | . . | . . |
| | Vert/transect unit | 45.6 | 31.5 | 47.9 | 29.0 | 29.4 | 35.6 | . . | . . | . . | . . | . . | . . |
| | Birds/transect unit | 44.1 | 30.0 | 46.4 | 28.8 | 29.1 | 35.2 | . . | . . | . . | . . | . . | . . |
| | Galliformes/tr unit | 13.6 | 5.7 | 10.2 | 7.1 | 3.3 | 5.6 | . . | . . | . . | . . | . . | . . |
| | Cal. Quail/tr unit | 8.2 | 0.8 | 4.9 | 5.0 | 2.4 | 3.9 | . . | . . | . . | . . | . . | . . |
| | Chukar/tr unit | 3.7 | 4.2 | 4.0 | 2.1 | 0.0 | 1.3 | . . | . . | . . | . . | . . | . . |
| | Gray Part./tr unit | 1.7 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | . . | . . | . . | . . | . . | . . |
| | Pheasant/tr unit | 0.0 | 0.8 | 0.3 | 0.0 | 0.9 | 0.4 | . . | . . | . . | . . | . . | . . |
| | Rabbits/tr unit | 0.6 | 0.2 | 0.4 | 0.1 | 0.2 | 0.2 | . . | . . | . . | . . | . . | . . |
| | Deer/tr unit | 0.6 | 1.2 | 0.8 | 0.0 | 0.0 | 0.0 | . . | . . | . . | . . | . . | . . |
| Winter | No. of Vert. Species | . . | . . | 42 | . . | . . | 21 | . . | . . | . . | . . | . . | . . |
| | No. of Bird Species | . . | . . | 39 | . . | . . | 21 | . . | . . | . . | . . | . . | . . |
| | Vert/transect unit | 92.3 | 119.7 | 119.7 | 40.6 | 39.6 | 46.3 | . . | . . | . . | . . | . . | . . |
| | Birds/transect unit | 92.3 | 119.7 | 118.3 | 40.6 | 39.6 | 46.3 | . . | . . | . . | . . | . . | . . |
| | Galliformes/tr unit | 16.7 | 10.9 | 14.1 | 10.7 | 4.3 | 7.9 | . . | . . | . . | . . | . . | . . |
| | Cal. Quail/tr unit | 12.1 | 2.3 | 7.8 | 9.0 | 1.5 | 5.8 | . . | . . | . . | . . | . . | . . |
| | Chukar/tr unit | 3.9 | 6.7 | 5.1 | 1.1 | 0.0 | 0.6 | . . | . . | . . | . . | . . | . . |
| | Gray Part./tr unit | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | . . | . . | . . | . . | . . | . . |
| | Pheasant/tr unit | 0.6 | 1.9 | 1.1 | 0.6 | 2.8 | 1.5 | . . | . . | . . | . . | . . | . . |
| | Rabbits/tr unit | 0.1 | 0.5 | 0.3 | 0.0 | 0.0 | 0.0 | . . | . . | . . | . . | . . | . . |
| | Deer/tr unit | 0.6 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | . . | . . | . . | . . | . . | . . |

[a]Only four transects (all other counts were with 16-24 transects).

[b]A transect unit equals 1.6 km or 1 mi.

TABLE 6. Road counts—seasonal comparisons among areas.

| Season | No. of censuses | Area[a] | Total species | Total indiv. | Ave. No. of species/census | Ave. No. of ind./census | H'[b] |
|---|---|---|---|---|---|---|---|
| SPRING | 2 | LGS | 40 | 983 | 30 | 492 | .93 |
| | 2 | LGN | 31 | 498 | 22 | 249 | .92 |
| | 2 | LGLM | 31(+2)[c] | 940 | 23 | 470 | .76 |
| SUMMER | 3 | LGS | 41 | 1084 | 31 | 361 | 1.15 |
| | 3 | LGN | 32 | 624 | 23 | 208 | 1.10 |
| | 3 | LGLM | 34(+3)[c] | 1041 | 23 | 349 | .99 |
| FALL | 2 | LGS | 33(+1)[c] | 411 | 25 | 206 | 1.12 |
| | 2 | LGN | 23 | 290 | 16 | 145 | 1.01 |
| | 2 | LGLM | 26 | 380 | 20 | 190 | 1.04 |
| WINTER | 4 | LGS | 39(+2)[c] | 673 | 22 | 170 | 1.09 |
| | 5 | LGN | 34 | 1283 | 16 | 256 | .85 |
| | 5 | LGLM | 32 | 881 | 15 | 176 | .88 |

[a]LGS (Lower Granite south side), LGN (Lower Granite north side), LGLM (Little Goose-Lower Monumental)

[b]Bird species diversity

[c]Species seen between stations, but not at any station

yearly totals of species and individuals as well as a yearly bird species diversity (BSD) index for the three different study areas. On the south side of Lower Granite Study Area, 69 species were recorded, whereas only 55 were seen on the Little Goose-Lower Monumental Study Area. The BSD index for the south side of Lower Granite Study Area was significantly higher (F test, analysis of variance) than the yearly index calculated for the Little Goose-Lower Monumental Study Area.

Results of road counts on the lowest 5 km (3 mi) of Steptoe and Wawawai canyon roads are also available (Lewke, 1975). Comparisons between these and post-impoundment data could be helpful in evaluating the capacity of draws to "absorb" birds displaced by the impoundment.

*Hunter Check Station Data.* A summary of data (from three stations) on hunter-killed game animals in 1972 and 1973 is presented in Table 8. Chukars were killed in the greatest numbers each year, and Ring-necked Pheasants and California Quail ranked second and third, respectively. In 1972, 525 game animals were shot, whereas only 260 were taken in 1975—more than a 50 percent reduction. The number of man-hours per animal (7.3 in 1972 and 16.3 in 1973) shows much greater hunter success in 1972 than in 1973.

As expected, parties hunting birds had higher success rates (33 percent and 46 percent) than parties hunting deer (31 percent and 7 percent). Bird hunters with dogs were more successful than those without dogs. Bird hunters spent 4.9 and 8.0 man-hours per bird killed in 1972 and 1973, respectively. Deer hunters had to hunt much longer for each animal shot—54.7 and 182.0 man-hours per deer in 1972 and

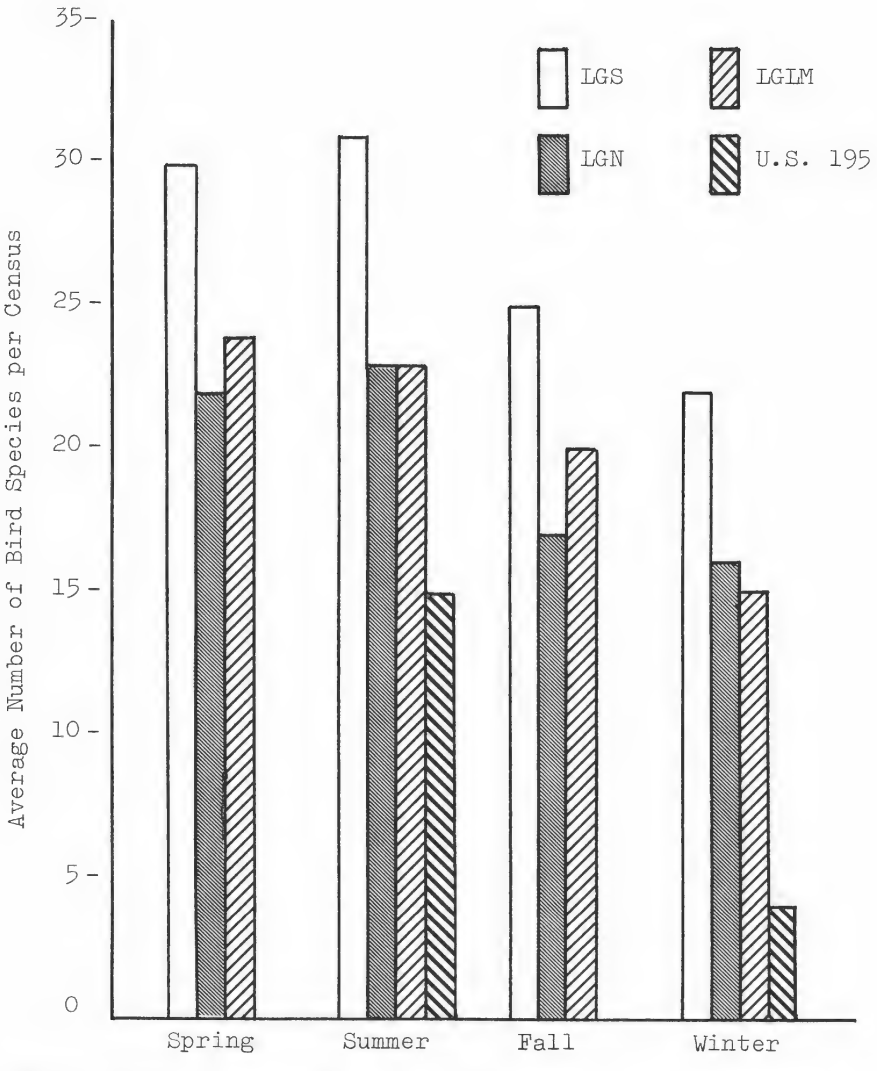



Figure 7. Average number of species per road count in Lower Granite south side, Lower Granite north side, Little Goose-Lower Monumental, and U.S. 195 (Colfax Highway) study areas.

1973, respectively. Of the 25 deer taken in 1972, species names of only 13 were recorded. All 13 were White-tailed Deer *(Odocoileus virginianus),* and all were taken in approximately the upper third of the canyon slopes and bluffs.

*Small Mammal Trapping Data.* The results of small mammal trapping on transects and in the Alpowa Creek Study Area are given in Tables 9 and 10, respectively. Both the actual number of each species caught and the number of trap-days per mammal are given.

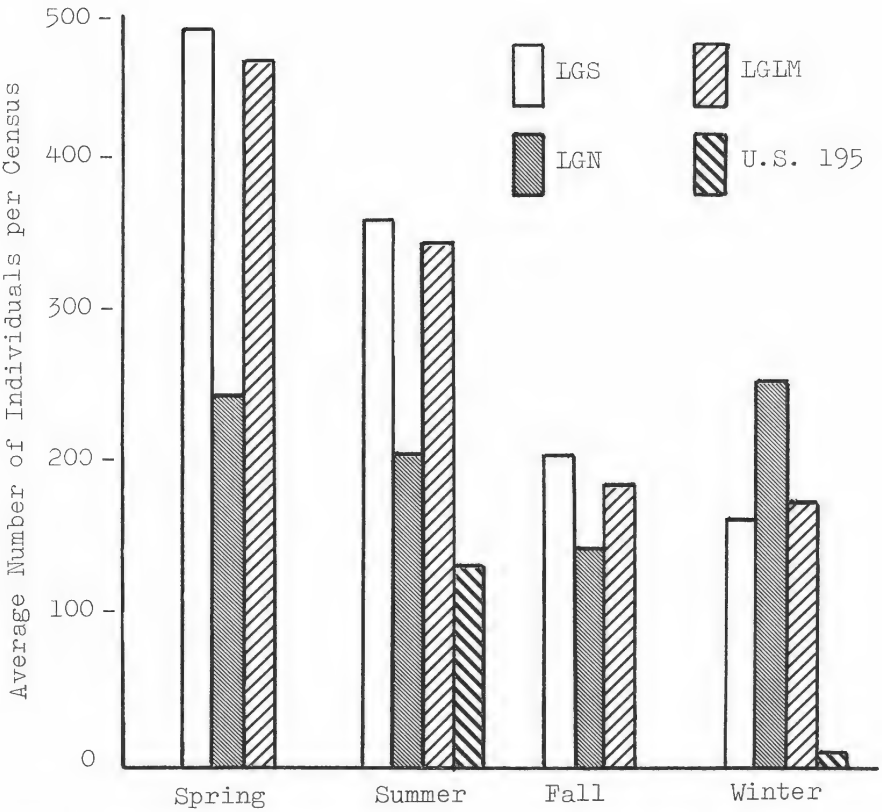



Figure 8. Average number of individuals per road count in Lower Granite south side, Lower Granite north side, Little Goose-Lower Monumental, and U.S. 195 (Colfax Highway) study areas.

Only three species of small mammals—*Peromyscus maniculatus, Perognathus parvus,* and *Reithrodontomys megalotis*—were trapped on the transects during the study period (fall, 1972-Spring, 1973). *Peromyscus maniculatus,* comprising 95 percent of the 201 mammals caught, was the most ubiquitous and abundant species trapped. Trapping success was greatest in spring (8.5 trap-days per mammal) and least in fall (34.2 trap-days per mammal). During all seasons trapping success was much greater during the night than the day (7.2 vs. 234.9 trap-days per mammal), revealing the primarily nocturnal habits of these small mammals.

Snap-trapping results from Alpowa Creek Study Area (Table 10) included four species not trapped on the transects—*Mus musculus, Microtus longicaudus, Microtus montanus,* and *Sorex vagrans.* No additional species were trapped with the live or sunken-can trapping methods. Again, *Peromyscus maniculatus* was the species most often trapped—representing 87 percent of the 113 mammals trapped. Future comparisons with these data will be impossible because the entire Alpowa study site has been flooded.

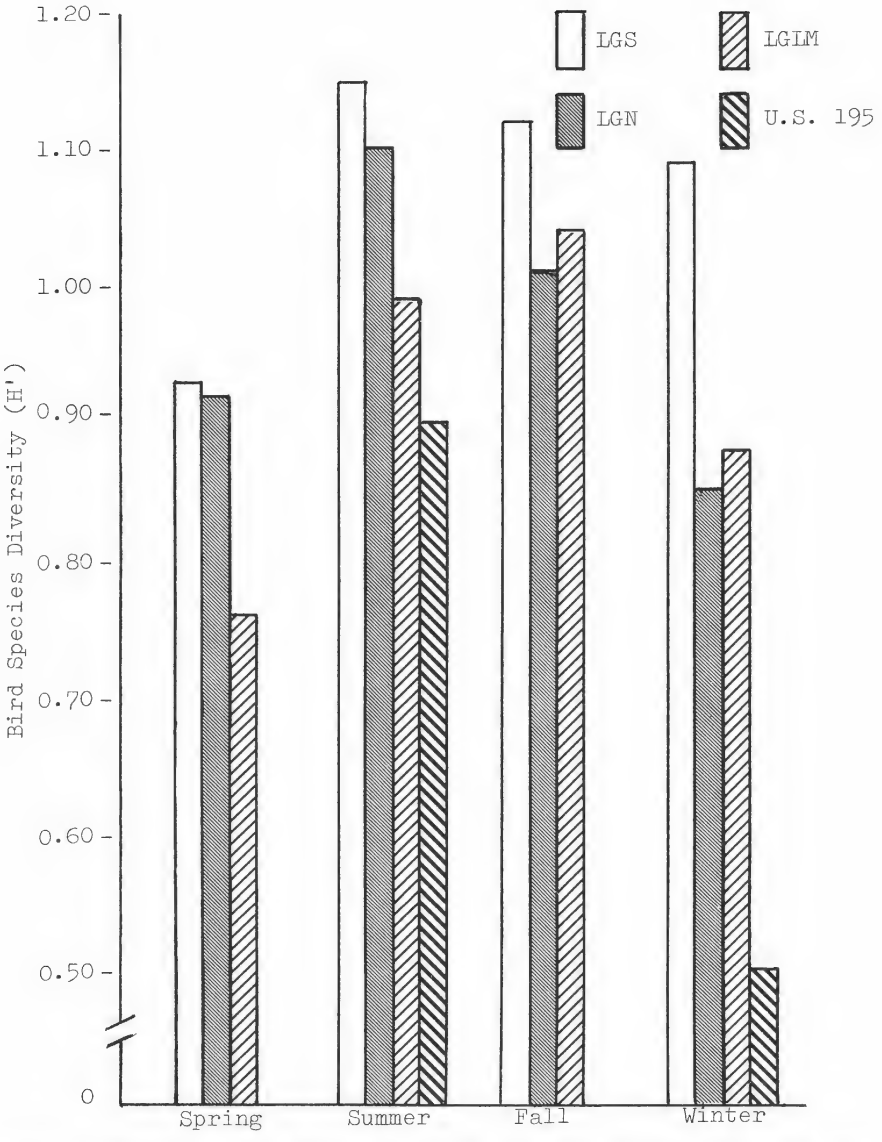



Figure 9. Average seasonal bird species diversity from road counts in Lower Granite south side, Lower Granite north side, Little Goose-Lower Monumental, and U.S. 195 (Colfax Highway) study areas.

*Habitat Preference Data for Birds*

Birds were seen below prospective pool level significantly more often than expected in all seasons except spring (Table 11). Even in spring, 51 percent of the birds were observed below pool level, indicating serious redistribution problems for birds in all

TABLE 7. Yearly road count totals for Lower Granite south side (LGS), Lower Granite north side (LGN), and Little Goose-Lower Monumental (LGLM) Study Areas.

| Category | LGS[a] | LGN | LGLM |
|---|---|---|---|
| Total No. of species | 69 | 53 | 55 |
| Total No. of individuals | 3147 | 2707 | 3261 |
| Yearly BSD[b] | 1.07** | 0.97 | 0.91** |

[a]Only 11 censuses, whereas the other two areas had 12.
[b]Average of monthly bird species diversity values.
**Significant difference between means (yearly averages) at the 1 percent level (F test).

TABLE 8. Data on hunter-killed game in Lower Granite Study Area (north side) in 1972 and 1973.[a]

| Category | 1972 | | 1973 | |
|---|---|---|---|---|
| All Game Animals | | | | |
| No. of parties | 375 | | 357 | |
| No. of successful parties | 150 | (40)[b] | 106 | (30) |
| No. of hunters | 821 | | 742 | |
| No. of hours spent hunting | 3801 | | 3755 | |
| No. of game animals shot | 525 | | 260 | |
| No. of man-hours/animals | 7.3 | | 16.3 | |
| Game Birds | | | | |
| No. of parties | 274 | | 213 | |
| No. of parties using dogs | 91 | (33) | 87 | (46) |
| No. of successful parties | 142 | (52) | 96 | (45) |
| No. of hunters | 587 | | 451 | |
| No. of hours spent hunting | 2433 | | 1939 | |
| No. of game birds shot: | | | | |
| Chukar | 297 | (59) | 165 | (68) |
| Ring-necked Pheasant | 92 | (18) | 29 | (12) |
| California Quail | 53 | (11) | 33 | (14) |
| Gray Partridge (Hun) | 31 | (6) | 14 | (6) |
| Mallard | 21 | (4) | 1 | (+) |
| Mourning Dove | 5 | (1) | 0 | (0) |
| American Wigeon | 1 | (+) | 0 | (0) |
| Redhead | 0 | (0) | 1 | (+) |
| Total | 500 | (99) | 243 | (100) |
| No. of birds shot by parties using dogs | 266 | (53) | 115 | (47) |
| No. of man-hours/bird | 4.9 | | 8.0 | |
| Rabbits (shot while bird hunting) | 0 | | 7 | |
| Deer | | | | |
| No. of parties | 101 | | 144 | |
| No. of successful parties | 21 | (21) | 10 | (7) |
| No. of hunters | 234 | | 289 | |
| No. of hours spent hunting | 1368 | | 1817 | |
| No. of deer shot: | | | | |
| Bucks | 17 | | 9 | |
| Does | 8 | | 1 | |
| Total | 25 | | 10 | |
| No. of man-hours/deer | 54.7 | | 182.0 | |
| Total number of days check stations were open | 30 | | 29 | |

[a]Data were collected at three game check stations operated on five weekends.
[b]Numbers in parentheses are percentages.

TABLE 9. Results of small mammal trapping on transects in Lower Granite Study Area in the fall (1972), winter (1972), and spring (1973).

| Season | Species | Total | Pool Level | | Period | | Capture Site Characteristics: Physiognomic type | | VG | G | F | S | M | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Above | Below | Night | Day | Non-ripar. | Ripar. | | Cover[a] | | | Soil Depth[b] | |
| Fall | *Peromyscus maniculatus* | 28 | 14 | 14 | 24 | 4 | 15 | 13 | . . | . . | . . | . . | . . | . . |
| | *Perognathus parvus* | 2 | 0 | 2 | 2 | 0 | 2 | 0 | . . | . . | . . | . . | . . | . . |
| | Total trapped | 30 | 14 | 16 | 26 | 4 | 17 | 13 | . . | . . | . . | . . | . . | . . |
| | No. of trap-days | 1025 | 461 | 564 | 512.5 | 512.5 | 517 | 508 | . . | . . | . . | . . | . . | . . |
| | No. of trap-days/mammal | 34.2 | 32.9 | 35.3 | 19.7 | 128.1 | 30.4 | 39.1 | . . | . . | . . | . . | . . | . . |
| Winter | *Peromyscus maniculatus* | 47 | 11 | 36 | 45 | 2 | 32 | 15 | . . | . . | . . | . . | . . | . . |
| | *Reithrodontomys megalotis* | 7 | 1 | 6 | 7 | 0 | 4 | 3 | . . | . . | . . | . . | . . | . . |
| | Total trapped | 54 | 12 | 42 | 52 | 2 | 36 | 18 | . . | . . | . . | . . | . . | . . |
| | No. of trap-days | 796 | 328 | 468 | 398 | 398 | 466 | 330 | . . | . . | . . | . . | . . | . . |
| | No. of trap-days/mammal | 14.7 | 27.3 | 11.1 | 7.7 | 199.0 | 12.9 | 18.3 | . . | . . | . . | . . | . . | . . |
| Spring | *Peromyscus maniculatus* | 117 | 39 | 78 | 117 | 0 | 53 | 64 | 30 | 44 | 51 | 59 | 25 | 33 |
| | No. of trap-days | 998 | 528 | 470 | 499 | 499 | 430 | 568 | 288 | 380 | 330 | 540 | 290 | 168 |
| | No. of trap-days/mammal | 8.5 | 13.5 | 6.0 | 4.3 | ∞ | 8.1 | 8.9 | 9.6 | 8.6 | 6.5 | 9.2 | 11.6 | 5.1 |
| All Seasons Combined | *Peromyscus maniculatus* | 192 | 64 | 128 | 186 | 6 | 100 | 92 | . . | . . | . . | . . | . . | . . |
| | *Perognathus parvus* | 2 | 0 | 2 | 2 | 0 | 2 | 0 | . . | . . | . . | . . | . . | . . |
| | *Reithrodontomys megalotis* | 7 | 1 | 6 | 7 | 0 | 4 | 3 | . . | . . | . . | . . | . . | . . |
| | Total | 201 | 65 | 136 | 195 | 6 | 106 | 95 | . . | . . | . . | . . | . . | . . |
| | No. of trap-days | 2819 | 1317 | 1502 | 1409 | 1409 | 1413 | 1406 | . . | . . | . . | . . | . . | . . |
| | No. of trap-days/mammal | 14.0 | 20.3 | 11.0 | 7.2 | 234.9 | 13.3 | 14.8 | . . | . . | . . | . . | . . | . . |

[a]VG = very good; G = good; F = fair.
[b]S = shallow; M = medium; D = deep.

TABLE 10. Results of small mammal trapping at the Alpowa Creek Study Area in the summer (June, 1973) and winter (early March, 1974).

| | | Capture Site Characteristics | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Period | | Physiognomic Type | | | | Cover[a] | | | Soil-Depth[b] | | |
| | | | | Non-Ripar. | | | Ripar. | | | | | | |
| Species | Total | Night | Day | Short weed field | Tall weed field | Sage flat | Weeds and shrubs | VG | G | F | S | M | D |
| *Peromyscus maniculatus* | 84 | 83 | 1 | 4 | 23 | 19 | 38 | 10 | 21 | 53 | 11 | 10 | 63 |
| *Mus musculus* | 4 | 3 | 1 | 0 | 4 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 4 |
| *Microtus longicaudis* | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Microtus* spp. | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 |
| Total trapped | 91 | 87 | 4 | 4 | 28 | 19 | 40 | 11 | 25 | 55 | 11 | 10 | 70 |
| No. of trap-days | 435 | 217.5 | 217.5 | 75 | 105 | 75 | 180 | 75 | 105 | 255 | 30 | 30 | 375 |
| No. of trap-days/mammal | 4.8 | 2.5 | 54.4 | 18.8 | 3.8 | 3.9 | 4.5 | 6.8 | 4.2 | 4.6 | 2.7 | 3.0 | 5.4 |
| Combined[c] | | | | | 5.0 | | | | | | | | |
| *Peromyscus maniculatus* | 15 | 15 | 0 | 1 | 1 | 1 | 12 | 0 | 3 | 12 | 2 | 0 | 13 |
| *Microtus montanus* | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 |
| *Sorex vagrans* | 5 | 2 | 3 | 0 | 1 | 0 | 4 | 0 | 1 | 4 | 0 | 0 | 5 |
| Total trapped | 22 | 18 | 4 | 2 | 2 | 1 | 17 | 0 | 5 | 17 | 2 | 0 | 20 |
| No. of trap-days | 435 | 217.5 | 217.5 | 75 | 105 | 75 | 180 | 0 | 270 | 165 | 30 | 30 | 375 |
| No. of trap-days/mammal | 19.8 | 12.1 | 54.4 | 37.5 | 52.5 | 75.0 | 10.6 | . . | 54.0 | 9.7 | 15.0 | ∞ | 18.8 |
| Combined | | | | | 51.0 | | | | | | | | |
| *Peromyscus maniculatus* | 99 | 98 | 1 | 55 | 24 | 20 | 50 | 10 | 24 | 65 | 13 | 10 | 76 |
| *Mus musculus* | 4 | 3 | 1 | 0 | 4 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 4 |
| *Microtus longicaudis* | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Microtus montanus* | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 |
| *Microtus* spp. | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 |
| *Sorex vagrans* | 5 | 2 | 3 | 0 | 1 | 0 | 4 | 0 | 1 | 4 | 0 | 0 | 5 |
| Total trapped | 113 | 105 | 8 | 6 | 30 | 20 | 57 | 11 | 30 | 72 | 13 | 10 | 90 |
| No. of trap-days | 870 | 435 | 435 | 150 | 210 | 150 | 360 | 75 | 375 | 420 | 60 | 60 | 750 |
| No. of trap-days/mammal | 7.7 | 4.1 | 54.4 | 25.0 | 7.0 | 7.5 | 6.3 | 6.8 | 12.5 | 5.8 | 4.6 | 6.0 | 8.3 |
| Combined | | | | | 9.1 | | | | | | | | |

[a]VG = very good; G = good; F = fair.
[b]S = shallow; M = medium; D = deep.
[c] = trap-days/mammal for non-ripar.

TABLE 11. Summary of avian habitat selection data (number of observations) from transect, road count, and Alpowa Creek studies.[a]

| Habitat | Spring No. | Spring % | Spring E%[b] | Summer No. | Summer % | Summer E%[b] | Fall No. | Fall % | Fall E%[b] | Winter No. | Winter % | Winter E%[b] | Total No. | Total % | Total E%[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Location | | | | | | | | | | | | | | | |
| Above pool level | 2000[c] | 49 | 48 | 826 | 46 | 53 | 858 | 50 | 57 | 1546 | 38 | 57 | 5230 | 45 | 54 |
| Below pool level | 2060[c] | 51 | 52 | 964 | 54 | 48 | 853 | 50 | 43 | 2506 | 62 | 43 | 6383 | 55 | 47 |
| Total | 4060 | 100 | 100 | 1790 | 100 | 101 | 1711 | 100 | 100 | 4052 | 100 | 100 | 11613 | 100 | 101 |
| Topographic Type | | | | | | | | | | | | | | | |
| Riverbank | 549 | 14 | 2 | 451 | 26 | 2 | 399 | 24 | 2 | 639 | 16 | 2 | 2038 | 18 | 2 |
| Floodplain | 1627 | 41 | 55 | 549 | 31 | 53 | 493 | 30 | 51 | 2033[c] | 50 | 51 | 4702 | 41 | 52 |
| Draw | 459[c] | 12 | 12 | 65 | 4 | 13 | 385 | 23 | 14 | 949 | 23 | 14 | 1858 | 16 | 13 |
| Cliff | 1314 | 33 | 31 | 690 | 39 | 32 | 367 | 23 | 33 | 424 | 11 | 33 | 2795 | 25 | 32 |
| Total | 3949 | 100 | 100 | 1755 | 100 | 100 | 1644 | 100 | 100 | 4045 | 100 | 100 | 11393 | 100 | 99 |
| Physiognomic Type | | | | | | | | | | | | | | | |
| Riparian | 1437 | 50 | 33 | 2623 | 50 | 32 | 1819 | 62 | 31 | 5316 | 63 | 31 | 11195 | 58 | 32 |
| Non-Riparian | 1419 | 50 | 67 | 2582 | 50 | 68 | 1115 | 38 | 69 | 3145 | 37 | 69 | 8261 | 42 | 68 |
| Total | 2856 | 100 | 100 | 5205 | 100 | 100 | 2934 | 100 | 100 | 8461 | 100 | 100 | 19456 | 100 | 100 |

[a]Alpowa Creek data used only for selection of physiognomic types because all sightings were below pool level and in riverbank-floodplain topographic types.
[b]Expected percentage from Tables 2 and 3.
[c]No significant difference between expected and observed values at the 1 percent and 5 percent levels (chi-square). All other differences are significant at 5 percent level or less.

seasons after the water level rose to the final impoundment level of 738 ft above MSL.

In a more discriminating analysis of habitat preference, topographic type was listed for each bird recorded. In all seasons, significantly more birds were seen in the riverbank habitat than expected, but fewer birds than expected were seen on the floodplain (Table 11). *Significantly, from 54-66 percent of all sightings were in riverbank-floodplain habitats, and practically all of these topographic habitats were destroyed by impoundment.*

Primary concern during this project has been focused on the importance of riparian vegetation to vertebrates in the valley. Data presented in Table 11 indicate that during all seasons a significant number of avian sightings were in the riparian physiognomic type. Of particular importance is the observation that in winter 63 percent of the 8,461 sightings were in this type of vegetation.

In Tables 12-16, data have been recorded by species (grouped as to residency; e.g., permanent, winter, summer, or migrant) for each season. Species frequently sighted in riparian and/or riverbank-floodplain categories have been marked with an asterisk. Species observed fewer than 10 times were not treated statistically but were marked with an "X" if they were believed to be dependent on riparian and/or riverbank-floodplain habitats. Expected values for chi-square tests were determined from percentages of habitat types given in Table 3.

Table 12 presents data on permanent resident sightings in nonriparian and riparian physiognomic types. Of the 36 species listed, 16 (44 percent) have significant riparian dependence during at least one season, and 7 (19 percent) have dependence during all seasons. In addition, four more species marked with an "X" probably are dependent upon riparian vegetation, but too few data prevent a stronger statement regarding dependence.

Table 13 presents the number of sightings of permanent resident species in riverbank-floodplain and draw-cliff topographic types. Fourteen of 36 species (39 percent) have significant dependence upon the riverbank-floodplain topographic types during at least one season of the year. Two more species (marked with an "X") probably are dependent, but again small sample size prevents a more conclusive statement about dependence.

The distribution of observations on summer resident species between physiognomic and topographic habitat types is presented in Table 14. Fifteen of 30 species (50 percent) show significant riparian dependence with three more species (marked with an "X") probably dependent. Dependency upon riverbank-floodplain topographic types is present in 10 to 30 species (33 percent) with one additional species probably dependent.

Data in Table 15 show that 11 of 26 winter resident bird species (42 percent) are dependent upon the riparian physiognomic type with five additional species (marked with an "X") probably dependent. Only two of 30 species (7 percent) are significantly dependent upon the riverbank-floodplain topographic types, and one additional species (marked with an "X") probably is dependent.

Information tabulated in Table 16 shows the distribution of migrant bird species among physiognomic and topographic types. Only three species were seen more than 10 times, with two of them showing significant riparian dependence. An additional nine species (marked with an "X") probably are dependent. Thus, 11 of 33 species (33 percent) show probable riparian dependence. Only four of 33 species (12 percent)

TABLE 12. Distribution (number of observations) of permanent resident birds (by species) within physiognomic types in Lower Granite Study Area.

| Species | Spring | | Summer | | Fall | | Winter | |
|---|---|---|---|---|---|---|---|---|
| | Non-ripar. | Riparian | Non-ripar. | Riparian | Non-ripar. | Riparian | Non-ripar. | Riparian |
| American Goldfinch | 66 | 193** | 17 | 56** | 42 | 41** | 211 | 215** |
| American Robin | 106 | 174** | 19 | 179** | 2 | 99** | 267 | 326** |
| Barn Owl | 0 | 3 X[a] | 0 | 6 X | 0 | 0 | 0 | 2 X |
| Belted Kingfisher | 2 | 2 X | 0 | 1 X | 1 | 1 X | 1 | 6 X |
| Black-billed Magpie | 58 | 94** | 39 | 54** | 17 | 54** | 45 | 105** |
| California Quail | 96 | 106** | 45 | 67** | 76 | 479** | 225 | 394** |
| Canada Goose | 24 | 1 | 0 | 0 | 1 | 0 | 12 | 0 |
| Canyon Wren | 36 | 3 | 27 | 1 | 57 | 7 | 80 | 7 |
| Cedar Waxwing | 0 | 3 X | 0 | 11** | 0 | 9 X | 0 | 1 X |
| Chukar | 205 | 93 | 30 | 40** | 70 | 41 | 73 | 59* |
| Common Crow | 1 | 0 | 0 | 0 | 0 | 0 | 5 | 0 |
| Common Flicker | 9 | 30** | 0 | 16** | 6 | 65** | 7 | 69** |
| Common Merganser | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Common Raven | 9 | 1 | 10 | 0 | 0 | 0 | 7 | 0 |
| Downy Woodpecker | 0 | 6 X | 0 | 6 X | 0 | 18** | 0 | 34** |
| Golden Eagle | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gray Partridge (Hun) | 3 | 6 | 0 | 0 | 15 | 0 | 0 | 0 |
| Great Blue Heron | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 1 |
| Great Horned Owl | 0 | 0 | 0 | 3 | 0 | 4 | 0 | 5 |
| Hairy Woodpecker | 1 | 2 X | 0 | 0 | 0 | 4 X | 0 | 7 X |
| Horned Lark | 0 | 0 | 0 | 0 | 0 | 0 | 193 | 0 |
| House Finch | 10 | 8 | 13 | 11 | 45 | 15 | 113 | 109** |
| House Sparrow | 16 | 32** | 30 | 12 | 40 | 9 | 17 | 18* |
| Mallard | 3 | 2 | 7 | 0 | 0 | 0 | 44 | 0 |
| Mourning Dove | 99 | 87** | 34 | 52** | 4 | 23** | 63 | 3 |
| Osprey | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Prairie Falcon | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Red-tailed Hawk | 10 | 2 | 2 | 0 | 0 | 1 | 1 | 3 |
| Ring-necked Pheasant | 58 | 34 | 26 | 13 | 45 | 38* | 71 | 23 |
| Rock Dove (Pigeon) | 24 | 3 | 25 | 0 | 17 | 28** | 5 | 12** |
| Rock Wren | 46 | 0 | 62 | 4 | 42 | 4 | 24 | 3 |
| Screech Owl | 1 | 3 X | 0 | 3 X | 0 | 0 | 0 | 1 X |
| Song Sparrow | 15 | 192** | 7 | 113** | 230 | 325** | 332 | 507** |
| Sparrow Hawk | 16 | 29** | 10 | 6 | 4 | 0 | 2 | 18** |
| Starling | 221 | 257** | 50 | 304** | 239 | 416** | 84 | 278** |
| Western Meadowlark | 282 | 71 | 74 | 1 | 87 | 2 | 110 | 7 |
| Total | 1419 | 1437 | 527 | 959 | 1045 | 1683 | 1993 | 2213 |

[a]Suspected of riparian dependence, but too few data to test statistically.

*Significance in favor of riparian dependence at 5 percent level (chi-square). Species with less than 10 observations/season are not treated statistically.

**Significant at 1 percent level (chi-square).

TABLE 13. Distribution (number of observations) of permanent resident birds (by species) within topographic types in Lower Granite Study Area.

| Species | Spring | | Summer | | Fall | | Winter | |
|---|---|---|---|---|---|---|---|---|
| | Riverbank-floodplain | Draws-cliffs | Riverbank-floodplain | Draws-cliffs | Riverbank-floodplain | Draws-cliffs | Riverbank-floodplain | Draws-cliffs |
| American Goldfinch | 36** | 7 | 21** | 2 | 35 | 26 | 317** | 6 |
| American Robin | 109 | 73 | 40** | 4 | 9 | 34 | 216 | 246 |
| Barn Owl | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Belted Kingfisher | 3 X[a] | 1 | 1 X | 0 | 2 X | 0 | 7 X | 0 |
| Black-billed Magpie | 72 | 82 | 95** | 13 | 18 | 14 | 50 | 65 |
| California Quail | 63* | 21 | 29** | 1 | 51 | 114 | 36 | 167 |
| Canada Goose | 23 | 6 | 0 | 0 | 0 | 0 | 12* | 0 |
| Canyon Wren | 1 | 40 | 3 | 25 | 11 | 48 | 6 | 79 |
| Cedar Waxwing | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Chukar | 86 | 213 | 42 | 34 | 41 | 75 | 49 | 87 |
| Common Crow | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 2 |
| Common Flicker | 18 | 6 | 5 | 1 | 25 | 16 | 12 | 12 |
| Common Merganser | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Common Raven | 2 | 9 | 6 | 6 | 0 | 0 | 0 | 7 |
| Downy Woodpecker | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Golden Eagle | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gray Partridge (Hun) | 4 | 3 | 0 | 0 | 0 | 15 | 0 | 0 |
| Great Blue Heron | 2 X | 0 | 0 | 0 | 5 X | 0 | 1 X | 0 |
| Great Horned Owl | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hairy Woodpecker | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| Horned Lark | 0 | 0 | 0 | 0 | 0 | 0 | 134** | 0 |
| House Finch | 7 | 7 | 3 | 1 | 11* | 0 | 133** | 3 |
| House Sparrow | 38** | 4 | 42** | 0 | 42** | 4 | 20 | 15 |
| Mallard | 8 | 0 | 7 | 0 | 0 | 0 | 55** | 0 |
| Mourning Dove | 79 | 34 | 36** | 5 | 25** | 1 | 61** | 1 |
| Osprey | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Prairie Falcon | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Red-tailed Hawk | 1 | 11 | 0 | 2 | 0 | 0 | 3 | 1 |
| Ring-necked Pheasant | 40 | 20 | 17** | 0 | 25** | 0 | 46** | 7 |
| Rock Dove (Pigeon) | 18 | 9 | 6 | 19 | 22 | 23 | 18 | 5 |
| Rock Wren | 2 | 46 | 10 | 55 | 13 | 35 | 2 | 25 |
| Screech Owl | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Song Sparrow | 36 | 10 | 20** | 2 | 81** | 20 | 174** | 26 |
| Sparrow Hawk | 27 | 18 | 2 | 10 | 4 | 1 | 7 | 5 |
| Starling | 219 | 151 | 74 | 51 | 93 | 78 | 143* | 86 |
| Western Meadowlark | 250** | 113 | 53** | 10 | 61** | 13 | 84** | 20 |
| Total | 1148 | 886 | 512 | 241 | 564 | 518 | 1589 | 867 |

[a]Suspected of riverbank-floodplain dependence, but too few data to test statistically.

*Significance in favor of riverbank-floodplain dependence at 5 percent level (chi-square). Species with less than 10 observations/season are not treated statistically.

**Significance in favor of riverbank-floodplain dependence at 1 percent.

TABLE 14. Distribution (number of observations) of summer resident birds (by species) within physiognomic and topographic types in Lower Granite Study Area.

| Species | Physiognomic Type | | Topographic Type | |
|---|---|---|---|---|
| | Non-ripar. | Riparian | Riverbank-floodplain | Draws & cliffs |
| American Coot | 0 | 0 | 0 | 0 |
| Bank Swallow | 50 | 0 | 92** | 0 |
| Barn Swallow | 0 | 0 | 0 | 0 |
| Black-chinned Hummingbird | 0 | 1 X[ab] | 0 | 1 |
| Black-headed Grosbeak | 0 | 57** | 3 | 2 |
| Brewer's Blackbird | 242 | 201** | 335** | 30 |
| Brown-headed Cowbird | 31 | 67** | 21** | 6 |
| Catbird | 0 | 12** | 1 | 0 |
| Cliff Swallow | 1113 | 0 | 219 | 1152 |
| Common Nighthawk | 1 | 0 | 2 | 0 |
| Eastern Kingbird | 2 | 25** | 8 X | 0 |
| Gulls | 27 | 3 | 33** | 0 |
| House Wren | 11 | 104** | 0 | 0 |
| Killdeer | 97 | 18 | 93** | 6 |
| Lark Sparrow | 37 | 13 | 20 | 7 |
| Lazuli Bunting | 47 | 161** | 42 | 50 |
| Northern Oriole | 20 | 176** | 103** | 11 |
| Red-eyed Vireo | 0 | 21** | 1 | 0 |
| Red-winged Blackbird | 305 | 425** | 465** | 9 |
| Rough-winged Swallow | 4 | 0 | 4 | 3 |
| Rufous-sided Towhee | 0 | 11** | 0 | 1 |
| Say's Phoebe | 12 | 3 | 6 | 2 |
| Sora | 0 | 1 | 0 | 0 |
| Spotted Sandpiper | 34 | 3 | 12** | 0 |
| Veery | 0 | 5 X | 0 | 0 |
| Western Kingbird | 15 | 43** | 41** | 2 |
| Western Wood Pewee | 2 | 27** | 4 | 0 |
| Willow Flycatcher | 0 | 2 X | 1 | 0 |
| Yellow-breasted Chat | 2 | 76** | 6 | 2 |
| Yellow Warbler | 3 | 209** | 43** | 7 |
| Total | 2055 | 1664 | 1555 | 1291 |

[a]Suspected of riparian or riverbank-floodplain dependence but too few data to test statistically.
[b]From Jewett *et al.*, 1953.
*Significance in favor of riparian or riverbank-floodplain dependence at 5 percent level. Species with less than 10 observations/season are not treated statistically.
**Significance in favor of riparian or riverbank-floodplain dependence at 1 percent level.

have been marked (with an "X") as probably dependent upon riverbank-floodplain topographic types.

All estimates of percentage of species dependence very probably are conservative, as several species were not recorded in a physiognomic or topographic type and yet were seen flying or swimming in the area. With more observations on these species, some of them certainly would have shown riparian and/or riverbank-floodplain dependence.

*Habitat Preference Data for Small Mammals*

Snap-trapping results presented earlier in Tables 9 and 10 show that *Peromyscus maniculatus* was by far the most numerous species caught (291 of 314, 93 percent). Figure 10 shows that this species has no observable preference for riparian vegetation during any season of the year. However, *P. maniculatus* does prefer a habitat with low (25 percent) cover value during the spring, summer, and particularly the winter. No data are available for the fall. Results on soil depth preference of this species are not clear. In spring, mice are more frequently caught in deep soil (30 cm) than in shallow

TABLE 15. Distribution (number of observations) of winter resident birds (by species) within physiognomic and topographic types in Lower Granite Study Area.

| Species | Physiognomic Type | | Topographic Type | |
|---|---|---|---|---|
| | Non-ripar. | Riparian | Riverbank-floodplain | Draws & cliffs |
| Bewick's Wren | 0 | 8 X[a] | 0 X | 0 |
| Black-capped Chickadee | 37 | 696** | 73 | 80 |
| Brown Creeper | 0 | 104** | 2 | 0 |
| Bufflehead | 0 | 0 | 0 | 0 |
| Common Goldeneye | 0 | 0 | 0 | 0 |
| Cooper's Hawk | 0 | 7 X | 0 | 2 |
| Dark-eyed Junco | 352 | 606** | 348 | 295 |
| Evening Grosbeak | 2 | 518** | 129** | 7 |
| Goshawk | 0 | 2 X | 0 | 0 |
| Golden-crowned Kinglet | 17 | 279** | 3 | 24 |
| Gray-crowned Rosy Finch | 1 | 0 | 1 | 0 |
| Hooded Merganser | 0 | 0 | 0 | 0 |
| Long-eared Owl | 0 | 1 X | 0 | 0 |
| Marsh Hawk | 4 | 5 | 2 X[b] | 1 |
| Mountain Chickadee | 1 | 56** | 6 | 0 |
| Northern Shrike | 1 | 3 X[b] | 2 | 0 |
| Pied-billed Grebe | 0 | 0 | 0 | 0 |
| Pine Siskin | 0 | 2 X | 0 | 0 |
| Rough-legged Hawk | 3 | 2 | 2 | 1 |
| Ruby-crowned Kinglet | 0 | 44** | 0 | 0 |
| Sharp-shinned Hawk | 0 | 13** | 2 | 1 |
| Short-eared Owl | 2 | 1 | 3 | 0 |
| Tree Sparrow | 4 | 0 | 0 | 0 |
| Varied Thrush | 0 | 26** | 3 | 0 |
| Whistling Swan | 0 | 0 | 0 | 0 |
| White-crowned Sparrow | 726 | 719** | 539** | 193 |
| Winter Wren | 2 | 11** | 1 | 0 |
| Total | 1152 | 3103 | 1116 | 604 |

[a]Suspected of riparian or riverbank-floodplain dependence but too few data to test statistically.
[b]From Jewett *et al.*, 1953.
**Significance in favor of riparian or riverbank-floodplain dependence at 1 percent level. Species with less than 10 observations/season are not treated statistically.

or medium depth soil. In summer the situation is reversed, and in winter, trapping success is greatest in shallow soil and least in medium depth soil.

Of the six species caught, only *Sorex vagrans* showed a possible preference for the riparian physiognomic type (4 of 5, or 80 percent caught in riparian habitat). *Mus musculus* seems to prefer weed fields, as the only four trapped were caught in this habitat. Too few data are available to indicate anything more than trends for these species.

Both *Microtus montanus* and *M. longicaudus* were trapped at the Alpowa study site. One *M. longicaudus* and two unidentified *Microtus* were trapped in summer, and two *M. montanus* were taken in winter. *Microtus* were caught in both riparian and non-riparian physiognomic types. All were taken in deep soil in each of the three cover classes.

*Loss of Game and Non-game Birds from Lower Granite Study Area*

Calculations were made from census data of riparian woodland and weedy-floodplain habitats at the Alpowa Creek Study Area on the number of individuals per 2.5 ha (1 a) per species for each type of habitat. These results are summarized in Table 17 for summer and winter populations. (See Lewke, 1975, for population data for individual species.)

TABLE 16. Distribution (number of observations) of migrant birds (by species) within physiognomic and topographic types in the Lower Granite Study Area.

| Species | Physiognomic Type | | Topographic Type | |
|---|---|---|---|---|
| | Non-ripar. | Riparian | Riverbank-floodplain | Draws & cliffs |
| Bald Eagle | 1 | 0 | 0 | 0 |
| Blue-winged Teal | 0 | 0 | 0 | 0 |
| Cinnamon Teal | 0 | 0 | 0 | 0 |
| Common Loon | 0 | 0 | 0 | 0 |
| Greater Yellowleggs | 0 | 0 | X[a] | 0 |
| Green-winged Teal | 0 | 0 | 0 | 0 |
| Harlequin Duck | 2 | 0 | 2 | 0 |
| Horned Grebe | 0 | 0 | 0 | 0 |
| Least Sandpiper | 0 | 0 | X | 0 |
| Lesser Scaup | 0 | 0 | 0 | 0 |
| Lewis' Woodpecker | 0 | 1 X | 1 | 0 |
| Lincoln's Sparrow | 1 | 0 | 0 | 0 |
| Long-billed Marsh Wren | 1 | 0 | 0 | 0 |
| MacGillivray's Warbler | 0 | 2 X | 0 | 0 |
| Nashville Warbler | 0 | 3 X | 0 | 0 |
| Olive-sided Flycatcher | 0 | 1 X | 0 | 0 |
| Pintail | 0 | 0 | 0 | 0 |
| Redhead | 0 | 0 | 0 | 0 |
| Ring-necked Duck | 0 | 0 | 0 | 0 |
| Ruddy Duck | 0 | 0 | 0 | 0 |
| Savannah Sparrow | 59 | 0 | 7 X[b] | 0 |
| Shoveler | 0 | 2 | 2 | 0 |
| Solitary Vireo | 1 | 0 X | 0 | 1 |
| Townsend's Solitaire | 0 | 3 | 1 | 1 |
| Townsend's Warbler | 0 | 4 X | 0 | 0 |
| Violet-green Swallow | 0 | 0 | 0 | 0 |
| Warbling Vireo | 0 | 3 X | 0 | 0 |
| Water Pipit | 2 | 0 | 1 X[b] | 0 |
| Western Flycatcher | 0 | 1 X | 0 | 0 |
| Western Tanager | 1 | 3 X | 1 | 1 |
| Wigeon | 0 | 0 | 0 | 0 |
| Wilson's Warbler | 0 | 18** | 1 | 0 |
| Yellow-rumped Warbler | 2 | 95** | 1 | 0 |
| Total | 70 | 136 | 17 | 3 |

[a]Suspected of riparian or riverbank-floodplain dependence but too few data to test statistically.

[b]From Jewett *et al.*, 1953.

**Significance in favor of riparian or riverbank-floodplain dependence at the 1 percent level (chi-square). Species with less than 10 observations/season are not treated statistically.

TABLE 17. Estimated summer and winter bird loss from inundation of riparian and weedy-floodplain habitats in Lower Granite Study Area.

| Season | Category | Riparian | | Weedy floodplain | | Total |
|---|---|---|---|---|---|---|
| | | No./40.5 ha | Res. loss[a] | No./40.5 ha | Res. loss | Res. loss |
| SUMMER | Permanent Residents | 894 | 4650 | 29 | 795 | 5445 |
| | Summer Residents | 1159 | 6194 | 87 | 2384 | 8578 |
| | TOTAL | 2053 | 10844 | 116 | 3179 | 14023 |
| WINTER | Permanent Residents | 1418 | 7373 | 414 | 11344 | 18717 |
| | Summer Residents[b] | 278 | 1445 | 0 | 0 | 1445 |
| | Winter Residents | 1532 | 7966 | 67 | 1836 | 9802 |
| | TOTAL | 3228 | 16784 | 481 | 13180 | 29964 |

[a]Number per hectare multiplied by the number of hectares lost by impoundment (210 riparian hectares and 1,109 weedy-floodplain hectares).

[b]A few summer residents were seen during the winter census period.

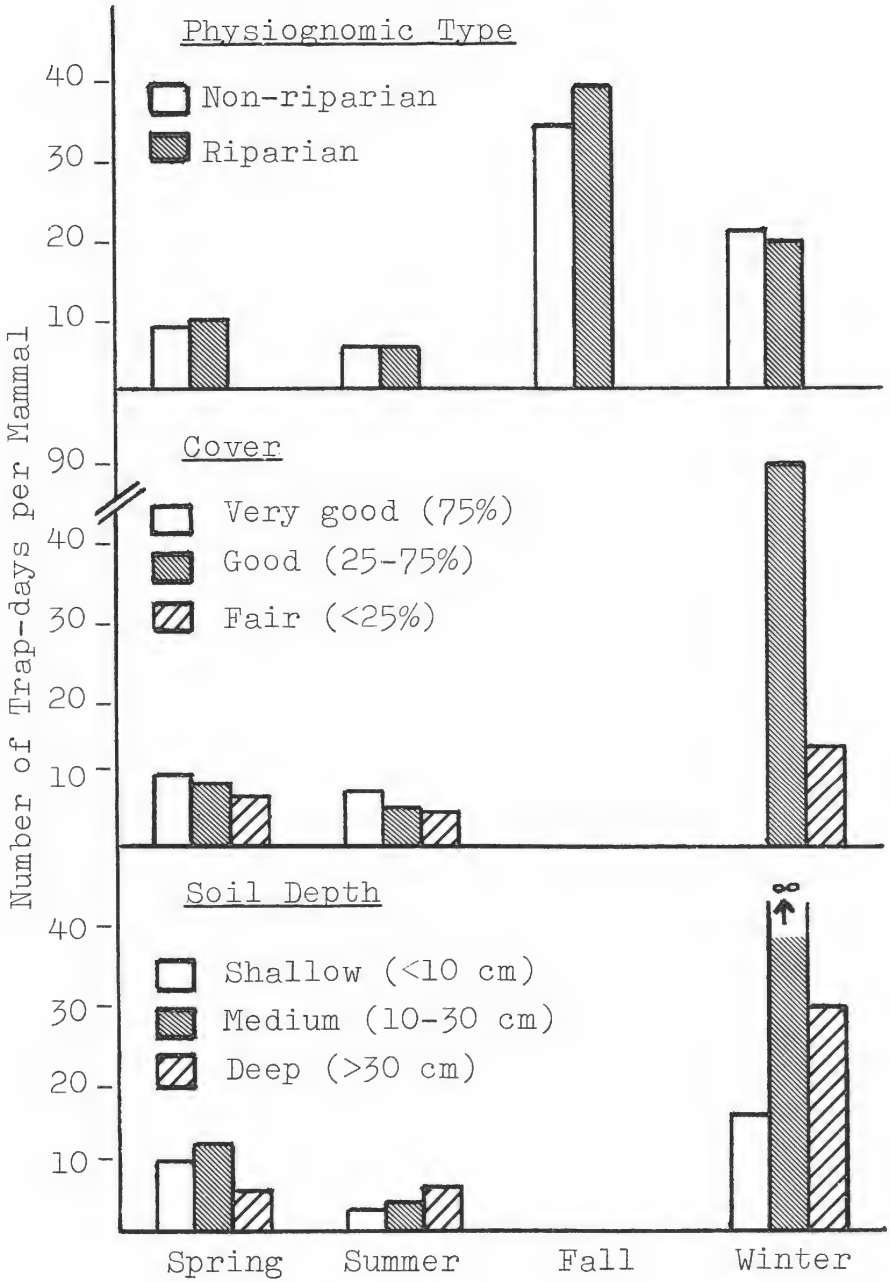



Figure 10. Habitat preferences of *Peromyscus maniculatus*.

The Corps of Engineers (1973, p. 30) calculated that 210 ha (520 a, 16 percent) of the total 1,319 ha (3,260 a) to be inundated were covered with trees, shrubs, and orchards (in the report referred to as "riparian habitat"). A check on these figures showed about 182 riparian ha (450 a, 14 percent) below prospective pool level. Because orchards had already been removed, this difference was expected. Since these calculations showed that the Corps' figures were very realistic, their values of 210 riparian ha (520 a) and 1,109 weedy-floodplain ha (2,740 a) (the difference between 1,319 and 210) were used to calculate the expected bird loss for the entire reservoir. These results are given as "total reservoir loss" in Table 17.

In summer, an estimated 10,844 birds will be lost from riparian habitat and 3,179 from weedy-floodplain habitat. Total summer loss from the impounded land is estimated to be over 14,000 birds. This figure is certainly conservative since no estimates of loss were possible for 15 species.

Total winter loss is estimated at nearly 30,000 birds. Of this winter total, 16,784 are from riparian habitat and 13,180 are from weedy-floodplain habitat. Again, these figures are conservative since no information was available for 18 species known to occur in the Snake River Valley in winter.

**Discussion and Conclusions**

*Habitat Destruction*

An estimate was made that showed a total of 1,319 ha (3,260 a) would be inundated when Lower Granite Reservoir was created. Of this total, 210 ha (520 a, 16 percent) represented riparian vegetation and 1,109 ha (2,740 a, 84 percent) were weedy-floodplain. What kind of habitat would be left after the reservoir was formed? Calculation based on aerial photographs showed that within the 63 km (39.1 mi) of reservoir, almost all riparian vegetation would be destroyed. Extensions of this vegetation remain in many of the draws, particularly on the south side of the river. (Fifteen of 45 draws or 33 percent on the north side of the river have been partially damaged from road relocation construction.

The weedy-floodplain habitat, with 1,109 ha (2,700 a, 54 percent) remaining, has survived better than the riparian habitat mentioned above. This amount, however, is misleading because of the 1,109 ha remaining, 769 ha (1,900 a, 70 percent) are at or upstream from Clarkston, Washington (*i.e.,* in the upper reaches of the reservoir).

From the above data, one can deduce that nearly 100 percent of the riparian habitat and 54 percent of the floodplain habitat between the dam and Asotin, Washington, were lost. Seventy percent of the remaining floodplain is upstream from Clarkston; thus, the 52 km (32 mi) between Lower Granite Dam and Clarkston has only 324 ha (800 a) of floodplain left.

Photographs show very clearly the severe habitat loss caused by the formation of impoundments. Figure 11 shows excellent riparian habitat along the southern bank of the Snake River in the Lower Granite Study Area. This vegetation, composed primarily of *Celtis reticulata, Salix* spp., and *Ribes aureum,* provides excellent habitat for California Quail, Black-billed Magpies *(Pica pica),* Yellow Warblers *(Dendroica petechia),* Northern Orioles *(Icterus galbula),* Vagrant Shrews *(Sorex vagrans),* and Muskrat *(Ondatra zibethicus),* to name a few. Figure 12, a photograph along the road that leads to Little Goose Dam, shows the complete absence of riparian vegetation at present.

Where no new roads were constructed, shorelines in the Lower Granite Study Area

Figure 11. Riparian vegetation along the southern bank of the Snake River in Lower Granite Study Area.

Figure 12. Shoreline along road count site in Lower Monumental Reservoir Study Area.

look much like those in Figure 13 along Little Goose Reservoir. Fluctuating water levels have caused severe bank-sloughing, since there is neither rocky shore nor deep-

Figure 13. Bank sloughing from fluctuating water levels in Little Goose Reservoir.

rooted vegetation to retain the soil. Needless to say, the amount and diversity of wildlife utilizing habitats pictured in Figures 12 and 13 cannot be as great as that using the riparian habitat shown in Figure 11. Support for this belief has been given in Tables 6 and 7, and Figures 7, 8, and 9.

Further evidence of severe habitat loss can be seen in Figures 14, 15, and 16, photographs depicting before tree-clearing, after tree-clearing, and post-impoundment of the Alpowa Creek Study Area. Terrestrial animals obviously will be forced to relocate. If we accept the fact that most habitats are nearly saturated with species (MacArthur, 1965), then we should not expect these displaced species to establish themselves in other habitats. Post-impoundment research would very probably support this contention. Furthermore, allowing for some territorial compression to occur—Kluyver and Tinbergen (1953) found it in populations of English titmice—a few displaced birds would probably move into habitats already occupied by conspecific individuals or occupy marginal habitats with relatively low carrying capacities.

*Importance of Riparian Habitats*

Data from transects have been presented in Table 5. Habitat saturation and possibly minor territorial compression suggest that the number of birds per transect-mile above pool level will stay about the same. Birds might move into draws to some extent, and this shift would increase the index. However, some bird species thought to be unaffected by the impoundment may be lost or reduced in abundance because of some undetected dependence on riparian habitat. This deduction, however, was found not to be true.

Transect data were collected during 1972 when road relocation had not yet destroyed

Figure 14. Alpowa Creek Study Area before tree clearing and before impoundment.

Figure 15. Alpowa Creek Study Area after tree clearing but before impoundment.

much of the habitat below pool level and during 1973 when habitat destruction was extensive. Consequently, an indication of what the loss of habitats below-pool level

Figure 16. Alpowa Creek Study Area after impoundment.

does to abundance of birds in the valley became impressively apparent. Figure 17 shows that except for above-pool indices in the spring, all 1973 indices are lower than those of 1972. (Although some variation in results from year to year can be caused by differences in abilities of students working on the transects, seasonal and year-to-year abilities were assumed to be similar.) The above- and below-pool indices in the winter show a greater than two-fold reduction in number of birds per 1.6 km transect from 1972 to 1973. Thus, three important points were revealed: (1) the weedy-floodplain and riparian habitats are extremely important to birds in winter; (2) the birds displaced from below-pool habitats will not permanently occupy above-pool habitats; and (3) the loss of below-pool habitats will cause a decrease in the number of birds found in above-pool habitats.

To predict the overall effect of the impoundment on bird populations, road counts were conducted along Little Goose and Lower Monumental Reservoirs as well as along both sides of the Lower Granite Study Area (see Fig. 1 and Table 6). Since the lower reservoirs were filled in 1969 and 1970, three to four years have elapsed, giving remaining bird populations time to stabilize. Counts along these reservoirs provided a basis for predicting what probably will occur in the Lower Granite Study Area after impoundment. Summer and winter counts along U.S. Highway 195 represent an extremely habitat-impoverished area for comparison.

Figures 7-9 illustrate graphically the important differences between results of road counts along the north and south side of Lower Granite Reservoir (LGN and LGS, respectively), Little Goose and Lower Monumental Reservoirs (LGLM), and U.S. Highway 195. Figure 7 shows that in all seasons LGS had the greatest number of species with LGN and LGLM having smaller numbers of species. These differences are interpreted as resulting from habitat destruction. No construction had taken place

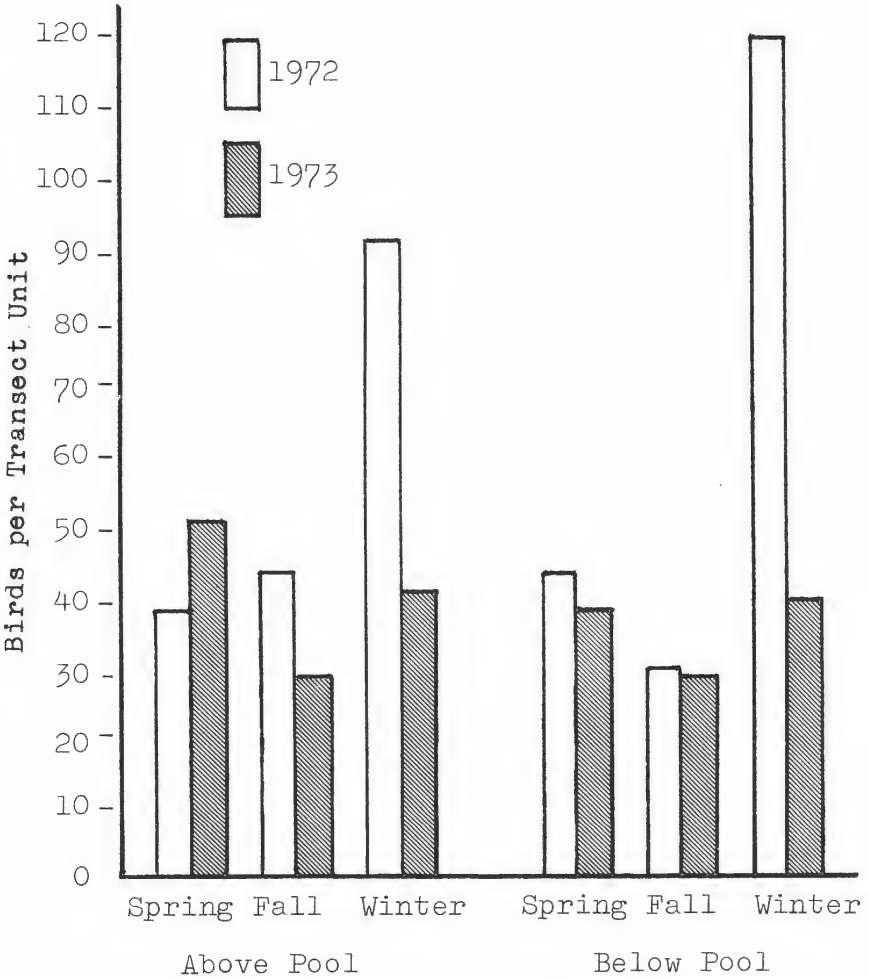



Figure 17. Decline in the number of birds per transect unit (1.6 km or 1 mile) from 1972 to 1973 on the north side of Lower Granite Study Area.

on the LGS site, whereas considerable damage from road relocation was taking place on the LGN site as this study was in its final year. The fact that the number of species observed in the LGN site was equal to or less than the number observed in the LGLM area in spring, summer, and fall indicates that disturbance caused by ongoing construction may be responsible for a temporary greater loss of species than will be caused by impoundment alone.

Figures 7 and 8 illustrate less difference in numbers of birds counted than in numbers of species seen in each area. Again, however, LGS had more birds than other sites in all seasons except winter. The high winter count for LGN is misleading since about 600 House Finches *(Carpodacus mexicanus)* and American Goldfinches *(Carduelis tristis)* seen together on one count greatly influenced the average value calculated for LGN

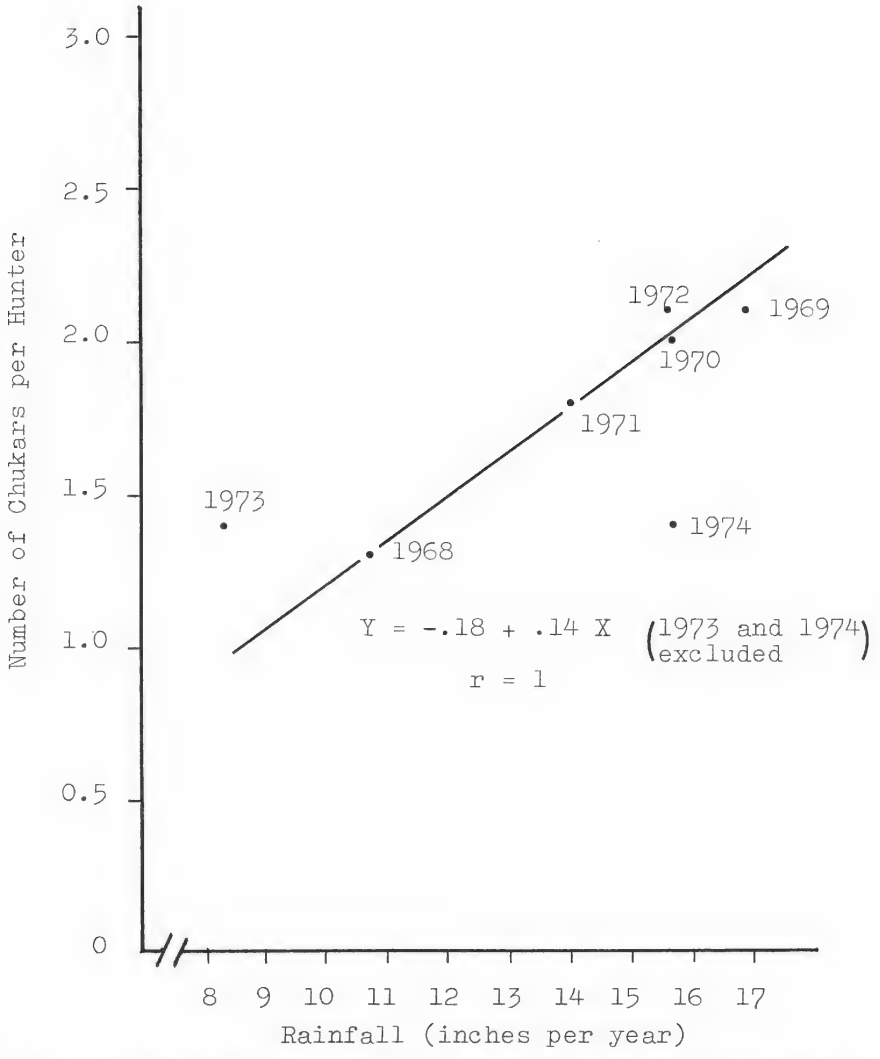



Figure 18. Correlation between rainfall and the number of Chukars shot per hunter from 1968-1972 on opening weekend of early Chukar season.

in the winter.

By combining both numbers of individuals and numbers of species, a very informative bird species diversity (BSD) index can be created. Diversity indices from Table 6 are illustrated graphically in Figure 9. Diversity indices for LGS are higher than all other sites in all seasons, and the yearly BSD indices (from Table 7) for LGS are significantly higher than those for LGLM. Yearly BSD indices from LGN are between those of LGS and LGLM and are not significantly different from either. After impoundment of Lower Granite Study Area, BSD values will almost certainly be more like

LGLM than LGS. Numbers of species and individuals, and bird species diversity in LGN may be temporarily higher in post-impoundment counts, since birds must move above pool level to escape the rising water. Several months more will be needed for stabilization to occur. This lowered BSD value indicates, according to MacArthur (1955), lowered community complexity, diversity, and perhaps stability.

Tables 12-16 show which avian species were observed significantly more often in either riparian (tree-shrub) physiognomic type or riverbank-floodplain topographic type. These data indicate which species of birds are closely associated with habitat types that will be lost or greatly reduced in acreage. Table 18, a summary of Tables 12-16,

TABLE 18. Avian dependence (in numbers of species) on riparian and riverbank-floodplain habitats.

| Residency | Dependence | |
|---|---|---|
| | Riparian | Riverbank-floodplain |
| Permanent | 20/36[a] (56)[b] | 16/36 (44) |
| Summer | 18/30 (60) | 11/30 (37) |
| Winter | 16/30 (53) | 3/30 (10) |
| Migrant | 11/33 (33) | 4/33 (12) |
| Total | 65/129 (50) | 34/129 (26) |

[a]Those species marked as suspected of dependence in Tables 21-25 are included as dependent species.
[b]Numerals in parentheses are percentages.

shows that 65 (50 percent) of 129 species are dependent upon the riparian physiognomic type, whereas 34 (26 percent) of 129 species are dependent upon the riverbank-floodplain topographic type.

All species that are dependent upon the riparian physiognomic type probably will not be lost since a few species will persist in riparian extensions in small tributary canyons. If, however, a species is dependent upon both riparian and riverbank-floodplain habitats, then this species is more likely to be forced out of the area. In Table 19, all species are listed that showed dependency on riparian and riverbank-floodplain habitats (see Tables 12-16), and the number of individuals are presented for each species seen in LGS, LGN, and LGLM. As expected, the yearly totals are highest for LGS (2,072 birds) and lowest for LGLM (1,678 birds), reflecting the effect of reduced riparian habitat in the latter area. For two reasons the difference between the two areas is actually greater than that shown: (1) only 11 censuses were taken in the LGS Study Area, but 12 were taken in the LGLM area; and (2) the large number of gulls (368 Ring-billed [*Larus delawarensis*] and California [*L. californicus*]) seen at the LGLM Study Area was a result of a large concentration at Little Goose Dam, not an even distribution along the length of the road count.

Species of birds that are very dependent upon the riverbank-floodplain topographic type (e.g., Western Meadowlark [*Sturnella neglecta*]), but are not dependent upon riparian vegetation, are abundant in the LGLM Study Area because floodplains are extensive in some places. Since floodplains will be almost completely destroyed in the Lower Granite Study Area, bird species dependent upon floodplain habitat will be drastically reduced after impoundment.

A list of birds seen on road counts in the LGS Study Area but not in the LGLM Study Area includes the following 26 species:

Permanent Residents
- Belted Kingfisher
- Downy Woodpecker

Summer Residents
- Black-headed Grosbeak
- Brown-headed Cowbird
- Catbird
- Say's Phoebe
- Western Wood Pewee
- Willow Flycatcher
- Yellow-breasted Chat
- Yellow Warbler

Winter Residents
- Black-capped Chickadee
- Brown Creeper
- Evening Grosbeak
- Gray-crowned Rosy Finch
- Hooded Merganser
- Mountain Chickadee
- Northern Shrike
- Rough-legged Hawk
- Varied Thrush

Migrants
- American Wigeon
- Lewis' Woodpecker
- Ruddy Duck
- Townsend's Solitaire
- Violet-green Swallow
- Water Pipit
- Yellow-rumped Warbler

Two additional species, Cooper's Hawk *(Accipiter cooperii)* and Common Loon *(Gavia immer),* were seen on LGN road counts and not on LGLM counts. This list further supports the conclusion that impoundment will decrease the number of species in the Lower Granite Study Area.

Another 39 species of birds were seen—15 on transects and 24 at the Alpowa Creek Study Area—in the Lower Granite Study Area and not in the LGLM Study Area. Transect and niche studies in the two lower reservoirs might have revealed the presence of some of these 39 species, but probably not many, because 21 of the 39 are classified as riparian dependent species (see Table 19).

In comparison to the list above, only 10 species were seen on LGLM road counts and not on LGS road counts. These species were the following:

Permanent Residents
- Gray Partridge
- Prairie Falcon

Summer Residents
- Barn Swallow
- Grasshopper Sparrow

Winter Residents
- Golden-crowned Kinglet
- Lesser Scaup

Migrants
- American Avocet
- Blue-winged Teal
- Green-winged Teal
- Pintail

Of these 10 species, only the Golden-crowned Kinglet *(Regulus satrapa)* is dependent upon the riparian physiognomic type. This kinglet is, in fact, much more abundant in the Lower Granite Study Area, but by chance was not recorded on any LGS or LGN road count. All other species listed above, except for the American Avocet *(Recurvirostra americana)* and the Grasshopper Sparrow *(Ammodramus savannarum),* were seen on transect or at the Alpowa Creek Study Area.

The following conclusions are from the data discussed above: (1) all bird species utilizing habitats below pool level will have their populations reduced; (2) the stronger the dependency of a species on riparian or floodplain habitats, the greater will be the impact upon that species' population losses; (3) since species will not be affected equally by habitat loss, population densities of each species will decline dispropor-

TABLE 19. Comparison of abundance of bird species dependent on riparian and riverbank-floodplain physiognomic and topographic types on the south and north side of Lower Granite Study Area (LGS and LGN) and in the Little Goose-Lower Monumental Study Area (LGLM).[a]

| Species | Dependency | | Study Area | | |
|---|---|---|---|---|---|
| | Riparian[b] | Riverbank-floodplain[c] | LGS[d] | LGN | LGLM |
| Permanent Residents | | | | | |
| American Goldfinch | yes | yes | 24 | 376 | 5 |
| American Robin | yes | yes | 60 | 81 | 7 |
| Barn Owl | X[e] | ? | 0 | 0 | 0 |
| Belted Kingfisher | X | X | 7 | 1 | 0 |
| Black-billed Magpie | yes | yes | 81 | 132 | 42 |
| California Quail | yes | yes | 62 | 31 | 2 |
| Cedar Waxwing | yes | ? | 0 | 0 | 0 |
| Chukar | yes | no | 64 | 111 | 36 |
| Common Flicker | yes | no | 21 | 16 | 4 |
| Downy Woodpecker | yes | ? | 1 | 0 | 0 |
| Great Blue Heron | no | X | 4 | 0 | 2 |
| Hairy Woodpecker | X | ? | 0 | 0 | 0 |
| Horned Lark | no | yes | 35 | 99 | 84 |
| House Finch | yes | yes | 19 | 140 | 99 |
| House Sparrow | yes | yes | 126 | 5 | 41 |
| Mallard | no | yes | 35 | 7 | 65 |
| Mourning Dove | yes | yes | 77 | 87 | 16 |
| Ring-necked Pheasant | yes | yes | 26 | 25 | 17 |
| Rock Dove | yes | no | 49 | 57 | 24 |
| Screech Owl | yes | ? | 0 | 0 | 0 |
| Song Sparrow | yes | yes | 134 | 68 | 48 |
| Sparrow Hawk | yes | no | 29 | 13 | 27 |
| Starling | yes | yes | 493 | 165 | 490 |
| Western Meadowlark | no | yes | 113 | 110 | 285 |
| Total Permanent Res. | . . | . . | 1347 | 1414 | 1009 |
| Summer Residents | | | | | |
| Bank Swallow | no | yes | 7 | 0 | 33 |
| Black-chinned Hummingbird | X | ? | 0 | 0 | 0 |
| Black-headed Grosbeak | yes | ? | 5 | 0 | 0 |
| Brewer's Blackbird | yes | yes | 183 | 17 | 50 |
| Brown-headed Cowbird | yes | yes | 3 | 11 | 0 |
| Catbird | yes | ? | 1 | 0 | 0 |
| Eastern Kingbird | yes | X | 5 | 2 | 3 |
| Gulls | no | yes | 13 | 21 | 368 |
| House Wren | yes | ? | 0 | 0 | 0 |
| Killdeer | no | yes | 31 | 15 | 20 |
| Lazuli Bunting | yes | no | 38 | 32 | 3 |
| Northern Oriole | yes | yes | 37 | 48 | 5 |
| Red-eyed Vireo | yes | ? | 0 | 0 | 0 |
| Red-winged Blackbird | yes | yes | 77 | 57 | 35 |
| Rufous-sided Towhee | yes | ? | 0 | 0 | 0 |
| Spotted Sandpiper | no | yes | 6 | 3 | 8 |
| Veery | X | ? | 0 | 0 | 0 |
| Western Kingbird | yes | yes | 21 | 7 | 11 |
| Western Wood Pewee | yes | ? | 3 | 0 | 0 |
| Willow Flycatcher | X | ? | 1 | 0 | 0 |
| Yellow-breasted Chat | yes | ? | 4 | 4 | 0 |
| Yellow Warbler | yes | yes | 29 | 7 | 0 |
| Total Summer Res. | . . | . . | 464 | 224 | 536 |
| Winter Residents | | | | | |
| Black-capped Chickadee | yes | no | 29 | 11 | 0 |
| Brown Creeper | yes | no | 2 | 0 | 0 |
| Cooper's Hawk | X | no | 0 | 1 | 0 |
| Dark-eyed Junco | yes | no | 88 | 83 | 5 |
| Evening Grosbeak | yes | yes | 60 | 6 | 0 |
| Goshawk | X | no | 0 | 0 | 0 |
| Golden-crowned Kinglet | yes | no | 0 | 0 | 1 |

TABLE 19. (Continued)

| | | | | | |
|---|---|---|---|---|---|
| Long-eared Owl | X | ? | 0 | 0 | 0 |
| Marsh Hawk | ? | X | 0 | 0 | 0 |
| Mountain Chickadee | yes | ? | 6 | 0 | 0 |
| Northern Shrike | X | ? | 1 | 1 | 0 |
| Pine Siskin | X | ? | 0 | 0 | 0 |
| Ruby-crowned Kinglet | yes | ? | 0 | 0 | 0 |
| Sharp-shinned Hawk | yes | ? | 1 | 0 | 1 |
| Varied Thrush | yes | ? | 1 | 0 | 0 |
| White-crowned Sparrow | yes | yes | 65 | 239 | 108 |
| Winter Wren | yes | ? | 0 | 0 | 0 |
| Total Winter Res. | . . | . . | 253 | 341 | 115 |
| Migrant Birds | | | | | |
| Greater Yellowleggs | no | X | 0 | 0 | 0 |
| Least Sandpiper | no | X | 0 | 0 | 0 |
| Lewis' Woodpecker | X | ? | 1 | 0 | 0 |
| MacGillivray's Warbler | X | ? | 0 | 0 | 0 |
| Nashville Warbler | X | ? | 0 | 0 | 0 |
| Olive-sided Flycatcher | X | ? | 0 | 0 | 0 |
| Savannah Sparrow | no | X | 5 | 2 | 18 |
| Solitary Vireo | X | ? | 0 | 0 | 0 |
| Townsend's Warbler | X | ? | 0 | 0 | 0 |
| Warbling Vireo | X | ? | 0 | 0 | 0 |
| Water Pipit | no | X | 1 | 0 | 0 |
| Western Flycatcher | X | ? | 0 | 0 | 0 |
| Western Tanager | X | ? | 0 | 0 | 0 |
| Wilson's Warbler | yes | ? | 0 | 0 | 0 |
| Yellow-rumped Warbler | yes | ? | 1 | 0 | 0 |
| Total Migrant Birds | . . | . . | 8 | 2 | 18 |
| Grand Total | . . | . . | 2072 | 1981 | 1678 |

[a]All data are from road counts.
[b]Riparian consists of shrub or tree-shrub vegetation (physiognomic types 7-10).
[c]Topographic types.
[d]LGS had only 11 censuses; LGN and LGLM had 12 censuses.
[e]Expected of being dependent, but too few data to test statistically.

tionately; (4) if the dependency is strong enough, the species may be completely forced out of the area; and (5) the lowered species diversity which results from points 1-4 probably will decrease community stability of the area, as suggested by MacArthur (1955).

*Estimates of Reservoir Bird Loss*

As stated above, birds found below prospective pool level will probably be unable to establish themselves in tributary canyons and cliff habitats left after impoundment. Data presented in Table 17 are estimates of the number of birds forced to abandon the below-pool habitats in summer and winter. Birds such as the Chukar, House Sparrow *(Passer domesticus),* and others that showed no loss (Lewke, 1975) may actually incur population losses even though they were never recorded on a census of riparian or weedy-floodplain physiognomic types at the Alpowa Creek Study Area. Most of these species have been seen at other times and areas in these habitats.

Two important points should be noted from Table 17. First, the paramount importance of riparian vegetation to birds in both summer and winter is obvious. Of the more than 14,000 birds estimated to be lost from the entire reservoir in the summer, about 11,000 (77 percent) are from riparian habitat, whereas over 3,000 (23 percent) are from the weedy-floodplain habitat. In winter, loss of riparian habitat ac-

counts for the loss of nearly 17,000 birds (56 percent), whereas more than 13,000 birds (44 percent) are lost because of weedy-floodplain loss. Secondly, the winter loss of nearly 30,000 birds is more than twice the summer loss of 14,000 birds. This statistic emphasizes the importance of the relatively warm valley as a wintering area for many species of birds. Many of these birds will be forced to find wintering areas elsewhere or perish. Winter and summer bird losses cannot be added to produce a yearly loss since permanent residents remain in the canyon throughout the year.

From Table 17 one can see that permanent, summer, and winter residents will all have heavy losses after impoundment, but what about migrant bird species? Very few individuals of any one species were observed in the valley. For example, the Yellow-rumped Warbler *(Dendroica coronata)* was seen most often (primarily one large flock at the Alpowa Creek Study Area), but not as often as expected on the basis of data collected in a deciduous woodland in Illinois (Lewke, unpub. field data). In spring, the leafing of *Celtis reticulata* and *Salix* spp. is not completed until May or early June. Since the migration peak of birds in this area is in May, the late development of *Celtis* and *Salix* leaves decreases the value of riparian habitat in the valley to migrating species. Perhaps migrants are more energy efficient if they continue flying over the valley instead of descending into it. This explanation does not seem to hold for the fall migration, since all trees retain their leaves through mid-October. However slight the use of riparian vegetation by migrants is, the loss of this vegetation will decrease even more the use of the valley as a resting spot for migrant bird species.

*Appraisal of Upland Game Birds*

Comparison of data from 1972 with data from 1973 (Table 8) reveals several trends which predict much poorer upland bird hunting in future years in the Lower Granite Study Area. Lower numbers of all four species of gallinaceous birds (Chuker, Ring-necked Pheasant, California Quail, and Gray Partridge) were shot in 1973 than in 1972. The number of pheasants shot showed the greatest decline (68 percent), and the number of quail shot declined least (38 percent). This difference can be explained by the habitat preference data presented in Tables 12 and 13. Quail are more closely associated with riparian habitat, whereas pheasants are more often found in weedy fields. Particularly in the fall and winter (hunting season), quail are seen much more often in ravines than on the floodplains; the reverse is true for the pheasant. Thus, in 1973, when road relocation destroyed large areas of floodplain, pheasants were forced to move to other locations (possibly across the river). If pheasants had moved up into above-pool habitats, they still would have been encountered by hunters, thus preventing such a sharp decrease in the number bagged. Quail, more abundant in the ravines than on the floodplain, were less affected by road construction than pheasants, and so the number of quail taken by hunters was not reduced as much from 1972 to 1973 as the number of pheasants.

The decline in quail bagged from 1972 to 1973 can be attributed primarily to the loss of riparian habitat in the riverbank-floodplain topographic type. Since quail are dependent upon riparian vegetation during all four seasons, retaining this vegetation in tributary canyons is paramount to quail survival. If these are cleared, quail populations will be totally lost. One needs only to look at the low number of quail (2) seen along Little Goose-Lower Monumental reservoirs to be convinced of the importance of

riparian habitat to California Quail. Ravines extending into these reservoirs have little or no riparian vegetation.

A more informative way to look at hunter-kill data is to calculate the number of man-hours per bird shot. This perspective allows a comparison of the two seasons regardless of the number of hunters checked each season. Even though 136 more hunters hunted (and were checked) in 1972 than in 1973, the number of man-hours per bird in 1972 was almost half that of 1973 (4.9 vs. 8.0). This figure shows that the decrease in number of hunters from 1972 to 1973 was not the main cause for the decline in number of birds shot. Again, habitat destruction is the main factor causing the decline.

Although Gray Partridge were taken less often by hunters in 1973 than in 1972 (14 vs. 31), the impacts of impoundment on this species are speculative. Two flocks of 15 and 7 birds were seen by students walking transects, but none were seen on road counts on either the north or south side of Lower Granite Study Area. Twenty-one were seen on counts in the LGLM Study Area. Yocom (1942) describes "Huns" as being common in fields, along fence rows, and in draws, but does not mention their status in the Lower Snake River Canyon.

The number of Chukars shot declined 46 percent from 1972 to 1973 (297 vs. 165). This species represented 59 percent and 68 percent of the upland game kill in 1972 and 1973, respectively, and is thus the most important upland game bird for hunters in the Lower Granite Study Area. The future of this species is of particular concern to hunters and, consequently, to the state game department.

Oliver (1968) believed that Chukar populations were reduced in the Ice Harbor Reservoir area because of the loss of riparian habitat after impoundment. He said that cover along the river provided safe breeding and drinking sites during the spring and summer months. In the Lower Granite Study Area, Chukars probably will not be as seriously affected by the loss of riparian and floodplain habitats as will the pheasant. Chukars depended significantly on riparian vegetation during summer and winter seasons (Table 12). At no time, however, were they found to be dependent upon that habitat within the riverbank-floodplain topographic type (Table 13). However, there may be some unknown aspects of the floodplain area which, although not recognized, do influence population numbers.

Data from road counts show that 36 Chukars were recorded in the LGLM Study Area, 64 in LGS, and 111 in LGN. The low number recorded in the LGLM Study Area probably was caused by lack of riparian vegetation remaining in draws.

If Chukars are as independent of below-pool habitats as indicated above, why was there a 46 percent decline in their numbers from 1972 to 1973? Several explanations are plausible. First, dependence upon or utilization of riparian and floodplain habitats is actually greater than this study detected. Secondly, 1973 may simply have been a low year in a fluctuating population; however, hunter-kill data, collected by the Washington State Game Department on opening week-end of early Chukar seasons from 1968-1974, do not support the presence of large population fluctuations in Chukars. Thirdly, low rainfall from September, 1972, through August, 1973, was possibly related to lower reproductive success. The correct explanation probably is a combination of the first and third explanations. These data do not support the idea that annual precipitation and reproductive success are related. Moreland (1950) indicated that water is a limiting factor for Chukars, and Oliver (1968) discussed its importance to Chukars in the

Ice Harbor area. Figure 18 shows a very strong positive correlation ($r = .998$) between amount of annual rainfall (from September to August) and number of Chukars shot per hunter for the years 1968 through 1972. Data from 1973 and 1974 were not used in the calculation of "r" because of road construction during these years. Hunter success was greater in 1973 than in 1968 even though rainfall was two inches less. This success may have been caused by a disruptive effect of heavy construction, which caused the Chukars to be more vulnerable to hunters. In 1974 high rainfall (15.6 in) did not produce the expected high populations as inferred from Chukar kill records. Therefore, the loss of below-pool habitats probably contributed to the lower Chukar populations, and therefore a lower number of Chukars were killed in 1974.

The following predictions can be made for the four species of upland game birds found in the Lower Granite Study Area: (1) all species probably will have their abundance reduced because of the loss of riparian and riverbank-floodplain habitats; (2) Ring-necked Pheasant populations will be reduced more than the other upland game birds because of their strong dependence upon floodplains which will be almost totally lost; (3) California Quail will rarely be found along the impoundment, but should still be common in draws with shrubby vegetation; (4) Chukars should still be abundant enough to provide good hunting; but (5) if rainfall is relatively low from September to breeding season, Chukar populations will probably be lower than in years of relatively high rainfall.

*Small Mammals*

From snap-trapping data collected on transects in 1972 and 1973, index figures (trap-days per mammal) were calculated (see Table 9). Mice were caught most frequently in below-pool habitats in all seasons except fall, and were caught equally as often in non-riparian physiognomic types as in riparian types. Using the same argument that was used for birds (species saturation and territorial compression), one would not expect many displaced mice to establish residency in above-pool habitats. Thus, there will be a loss of large numbers of small mammals from the present population. The impact this loss will have on predators of small mammals is unknown. If hawks, falcons, and owls can hunt the ravines, bluffs, and plateaus without having to range widely, then they should continue to nest in the ravines and canyon cliffs. Road counts along Little Goose and Lower Monumental reservoirs revealed the presence of Red-tailed Hawks *(Buteo jamaicensis),* American Kestrels *(Falco sparverius),* Prairie Falcons *(Falco mexicanus),* and Great Horned Owls *(Bubo virginianus),* thus indicating that these species have been able to adapt to an area that has lost its riparian habitat and part of the floodplain.

Trapping results from the Alpowa Creek Study Area (Table 10) show that only *Sorex vagrans* seems to be dependent upon riparian vegetation since four of five (80 percent) were caught in this habitat. More data obviously are needed to confirm this dependence. *Mus musculus, Microtus montanus,* and *Microtus longicaudus* were never trapped in draws by students, yet they were trapped in the Alpowa floodplain. Although the data are meager, they tend to suggest that these species may be seriously affected by the impoundment since virtually all the floodplain will be destroyed.

Certainly, all individuals living on the floodplain will be lost or displaced. If, as MacArthur (1955) suggests, most habitats (e.g., the habitats above pool level) already are saturated with animal populations, then a number of individuals equivalent to that

of the floodplain populations will be lost. This number probably would include raptorial birds and carnivores dependent for food on small mammals of the floodplain habitats.

*Conclusions*

What can be done in the Lower Granite Study Area to compensate for wildlife losses caused by the impoundment behind Lower Granite Dam? The answer, unfortunately, is very little. Nearly all the floodplain, with its deep soil, is now under water. The thick riparian and weedy-floodplain vegetation that grew on this land cannot be planted above the present pool level, because soil on the steep slopes is shallow or nonexistent, and water is less accessible to plants. The best that can be hoped for is that the vegetation in ravines will be left for wildlife. Without it, many permanent residents of the valley will be forced to other areas, many summer residents will not be able to breed in the valley, many winter residents will be forced to find refuge elsewhere, and migrants (other than waterfowl) will not have cause to stop temporarily in the valley. In short, what once was an area with varied and abundant habitat has had most of its valuable riparian and floodplain habitat destroyed, thus resulting in a significant and permanent loss of wildlife.

The following list summarizes the important observations and conclusions on the impacts of impoundment on vertebrate (mainly avian) populations in the Lower Granite Study Area:

1. Nearly 100 percent of the floodplain between Lower Granite Dam and Clarkston, Washington, was inundated.
2. Of the 1,319 ha (3260 a) inundated, 210 ha (520 a, 16 percent) represented valuable riparian habitat, and 1,109 ha (2,740 a, 84 percent) represented weedy-floodplain habitat.
3. Riparian and weedy-floodplain habitats are important to birds during all seasons, but particularly in winter.
4. Evidence obtained by this study forces the conclusion that most displaced birds will not be able to re-establish themselves in remaining above-pool habitats.
5. The loss of below-pool habitats indirectly will cause a decrease in the number of birds remaining in above-pool habitats.
6. Bird species diversity will decrease in the Lower Granite Study Area after impoundment.
7. Sixty-five (50 percent) of the 129 bird species observed were found to be significantly dependent upon the riparian (tree-shrub) physiognomic type.
8. Thirty-four (26 percent) of the 129 bird species were found to be significantly dependent upon the riverbank-floodplain topographic type.
9. The greater a species' dependence on riparian or riverbank-floodplain types, the greater the effect of impoundment on that species.
10. Impoundment is estimated to cause the loss locally of over 14,000 birds in summer and 30,000 birds in winter.
11. Migrant species of birds (excluding waterfowl) did not utilize the Lower Snake River Canyon habitats to a great degree and thus will not be affected nearly as much as permanent, summer, and winter resident species.
12. Populations of all upland game species will decrease after impoundment, with Ring-necked Pheasant populations being reduced the most because of this species' strong

dependence upon the floodplain.

13. Since different species will not be affected equally by habitat loss, population density of each species will decline disproportionately.
14. Although Chukar hunting success, which is positively related to annual rainfall, declined 46 percent from 1972 to 1973, this upland game bird will maintain high enough population densities to provide good hunting in future years.
15. *Mus musculus, Microtus montanus,* and *M. longicaudus* populations may be severely reduced because of the loss of floodplain habitat. Such a loss of small mammals could have a significant impact on the composition and function of the entire ecosystem in which these animals lived.

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# Water Potential in Sagebrush and Shadscale Communities

## Abstract

Predawn soil and plant water potentials within big sagebrush/galleta grass, and shadscale/galleta grass communities were measured with the aid of Peltier psychrometers. Soil water potentials varied among depths and communities, but differences were not consistent throughout the study period. Plant water potentials of big sagebrush, shadscale, Douglas rabbitbrush and galleta grass varied significantly ($P$ 0.1) during the growing season. Big sagebrush and shadscale water potentials were consistently lower than those of galleta grass or rabbitbrush. Differences in physiology and root distribution appear partially to explain variations in water potential among species.

## Introduction

Water potentials significantly influence water movement within the soil plant atmosphere system and physiological processes in plants (Hsieh *et al.,* 1972; Wiebe, 1972). As such, plant water potentials provide information on the relationship of species to the site and interrelationships among species. Wiebe *et al.* (1970), Hsieh *et al.* (1971), Moore and Caldwell (1972), and Halvorson and Patten (1974) studied water potentials of species in juniper, sagebrush, shadscale, and creosote brush communities, respectively.

Water potentials in the soil-plant system of sagebrush and shadscale communities have not been studied in detail, nor have they been compared between adjacent communities.

Plant and soil water potentials within sagebrush (*Artemisia tridentata* Nutt.)/galleta grass (*Hilaria jamesii* (Torr.) Benth.) and shadscale (*Atriplex confertifolia* (Torr. and Frem.) Wats.)/galleta grass communities as determined by Peltier psychrometers are presented here. Water relations among species within a community and within a species between communities are considered. Root distribution and water potential gradients within the soil profiles were also studied.

## Description of Area

The study was conducted in Hot Creek Valley, Nevada, in the southwest portion of the Great Basin. The area has a semiarid climate with mean annual precipitation of 13.5 cm. Precipitation for the study year, 1972, was 13.2 cm. Shadscale/galleta grass and

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sagebrush/galleta grass communities dominate the study area. Two study sites were established 1.2 km apart in exclosures protected from grazing for four to eight years. The sagebrush and shadscale communities occurred on the midportion of a dissected pediment fan (elevation 1,960 m), and an alluvial terrace (elevation 1,740 m), respectively.

### Methods and Materials

*Psychrometers and Calibration:* Commercially built EMCO[2] double-junction thermocouple psychrometers were used in this study. Psychrometers were calibrated in a teflon calibration chamber (EMCO) and also in the polypropylene sample chambers (internal volume 3.5 $cm^2$) used in the field. Psychrometers were calibrated over NaCl solutions having water potentials ranging from -4 to -94 bars and at various temperatures in the 10° to 30° C range to derive standard reference curves (Wiebe *et al.,* 1971).

*Soil and Plant Water Potentials:* The seasonal progression of water potentials in the soil-plant systems of sagebrush and shadscale communities was measured from June through September of 1972. Species were selected for study because they were either dominant in a community or a major component of both communities. Water potentials of sagebrush, shadscale, galleta grass, and rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.) were measured.

A preliminary field study, conducted in April, 1972, indicated that 10 samples per species adequately sampled the population when the 0.1 probability level was used to determine differences. The 30 samples required for the 0.05 probability level were considered excessive for our resources.

Ten plants of each species were permanently identified at each site. Sets of three species close together were chosen to reduce differences in microclimate within each location. The same plants were sampled throughout the study to avoid genetic and microclimate variability among samples.

Water potentials of plants and soils were measured in the predawn hours, as Klepper (1968) and Brown (1974) suggested. Constant sampling conditions and reduced ambient temperature variations were thus obtained during the sampling and equilibration period. Collection of plant material was made as simple as possible to facilitate predawn collecting. Grass blades and young culms were picked at random in the marked clones. Blades of grass were folded once and the cut end placed away from the thermocouple junction. Shrub samples contained small stems and attached leaves. Leaves remained intact and the cut end of the stem was placed away from the thermocouple junction. To measure plant water potential for each species, we sampled 10 plants at the same time.

Psychrometer chambers were filled with the plant materials. Care was taken to have plant materials close to but not touching the thermocouple junctions. Close proximity of the evaporative surface and psychrometer is required to insure a common temperature and adequate diffusion (Manohar, 1966; and Miller *et al.,* 1970). The chambers were placed in a styrofoam box and the samples were allowed to equilibrate with the chamber air for 1.5 h. Equilibration periods of 0.5 h and 3 h were compared on several occasions during the study.

[2] Use of trade or firm names is for reader information only, and does not constitute endorsement by the U.S. Department of Agriculture of any commercial product or service.

Concurrent measurements of soil water potentials and temperatures were made with in situ soil psychrometers protected by mesh screens. Psychrometers were buried at depths of 14, 30, and 60 cm.

*Root Photography in situ:* Several plants of each species were excavated from each community to aid in interpreting measured soil and plant water potentials. Exposed roots were sprayed with paint from pressurized cans (Shultz and Biswell, 1955), and the adherent soil was removed with water. The root systems of these plants were then photographed.

*Statistical Methods:* A randomized complete block design was used to evaluate plant water potentials in each community. If significance was found in the analysis of variance, Duncan's multiple range test was used to determine which species or ecotypes were significantly ($P$ 0.1) different. For purposes of analysis, plant water potentials for big sagebrush and shadscale were set at -70 bars when their values exceeded the range of the psychrometers.

Soil water potentials at the various depths were compared within and between communities. The $P$ 0.05 level was used in the analysis of variance.

**Results and Discussion**

*Soil and Water Potentials:* Early morning soil water potentials and temperatures were not significantly ($P$ 0.05) different over time at depths of 15, 30, and 60 cm within and between the community types. Water potentials within the soil profiles of the communities varied from near 0 to -70 bars during the study (Figs. 1 & 2). Soil temperatures increased rapidly in June, reached a July-August plateau and then declined slowly through September (Fig. 3). Soil temperature and water potential gradients opposed each other in some instances, but most often indicated probable vapor and water movement through or into the 30-cm zone.

*Root Bisect:* Strain (1970), Love and West (1972), and Halvorson and Patten (1974) postulated that the root systems of species they studied influenced the plant water potential. Rooting characteristics of rabbitbrush and galleta grass differed between the shadscale and sagebrush communities (Fig. 4). Rooting depth of rabbitbrush was greater than that of galleta grass in the big sagebrush community, but rooting depths of these species were the same in the shadscale community. Rooting depth of galleta grass was similar in both communities. Rooting characteristics of the studied shrubs were similar, but sagebrush had a greater rooting depth. Root density of the studied species was generally greatest at about 30 cm, suggesting that increased competition for water occurs in this zone.

*Plant Water Potentials:* Psychrometer data from excised plant materials approximate water potential values in the living plant. Variations in distance of psychrometer junction to leaf sample and small temperature gradients within the chamber may have scattered measurements slightly. Surface dirt and secreted salts on plant materials may have affected water potential readings of the samples to some degree; however, even with such errors, the measurements are still useful in showing relative changes over time.

The 1.5 h equilibration period appeared adequate for galleta grass and rabbitbrush. The "time course" curve of psychrometer readings (Klepper and Barrs, 1968) leveled off after 1.5 h in most instances. Water potential values were 4 to 8 bars higher after equilibrating for 3 h, but whether this difference more closely represents actual water potential or post sampling changes in leaf tissue is not known.

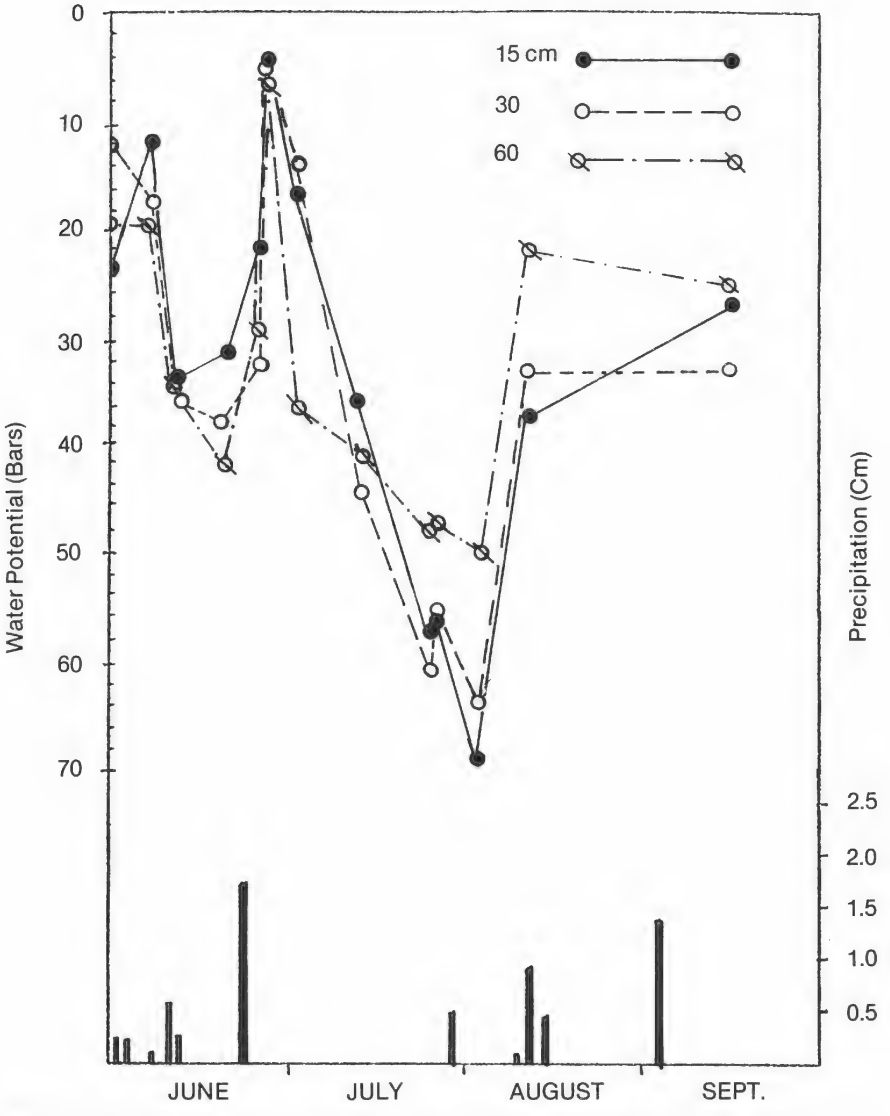


Figure 1. Seasonal soil water potential at depths of 15, 30, and 60 cm in the shadscale community (1972).

Plant water potentials reflect the environment in which the plant is growing and will change for any xerophytic species with time and space. Plant water potentials for all species varied significantly ($P$ 0.1, 0.05) during the study period (Figs. 5 & 6). Water potentials of big sagebrush and shadscale were significantly (0.5) lower than those of rabbitbrush or galleta grass in the same community. Similar findings were reported for sagebrush and rabbitbrush by Hsieh *et al.*, 1971.

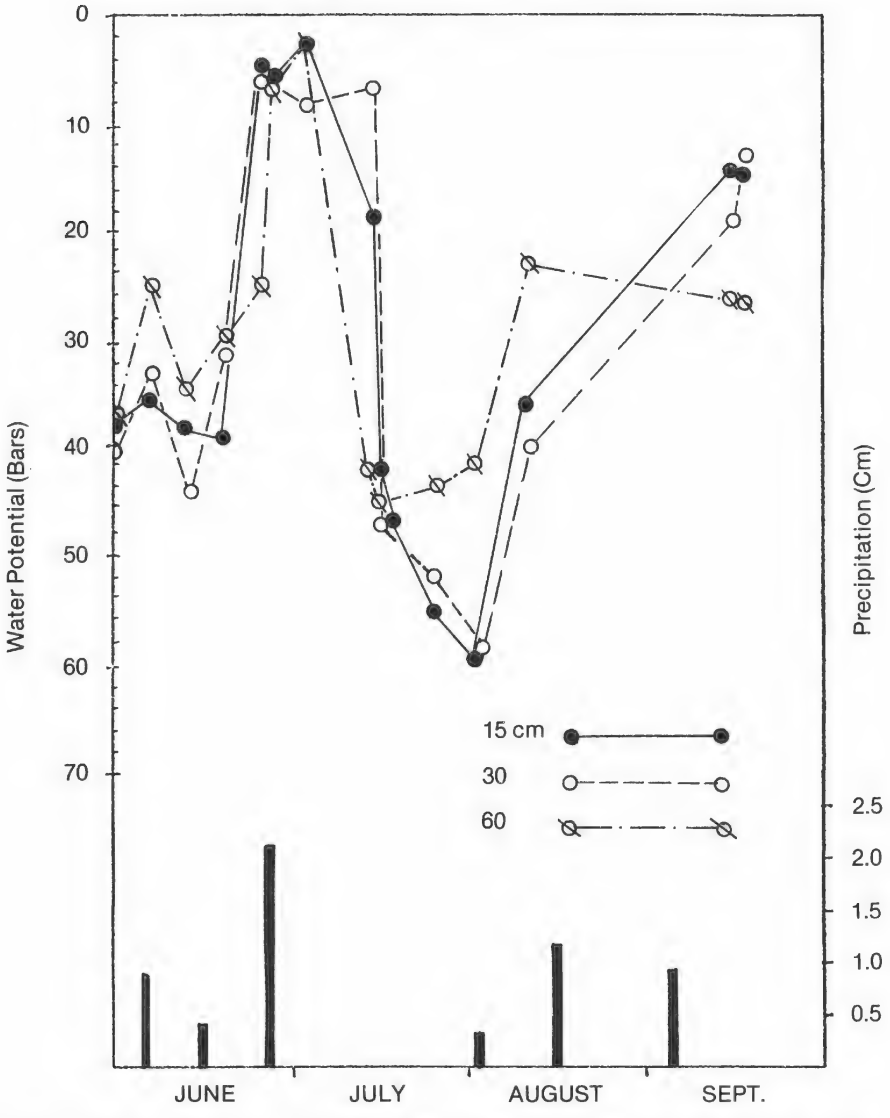


Figure 2. Seasonal soil water potentials at depths of 15, 30, and 60 cm in the upper big sagebrush community (1972).

Peltier psychrometers were not capable of adequately measuring the seasonal water potential changes in shadscale or sagebrush under existing site conditions. Pressure bomb derived water potentials have been reported for sagebrush, both above (DePuit and Caldwell, 1973) and below (Dian, 1970) the psychrometer values reported here. Moore and Caldwell (1972) and Love and West (1972) reported water potentials of shadscale that were within psychrometric range; but it is unlikely that total osmotic potential was

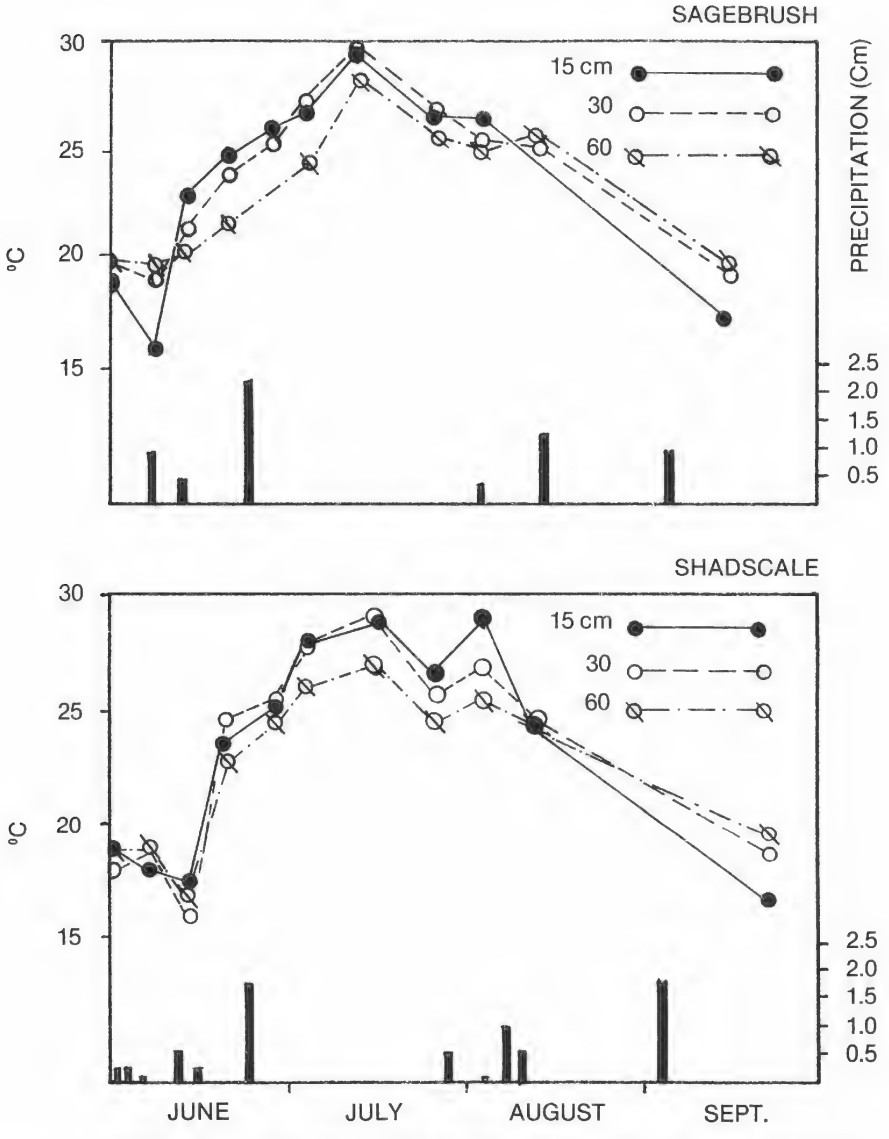


Figure 3. Seasonal pattern of soil temperature at depths of 15, 30, and 60 cm in sagebrush and shadscale communities (1972).

measured. Seasonal patterns in water potential observed for these species were similar to those reported by the persons cited above.

Low water potentials of sagebrush were perhaps due in part to its inability to control transpiration adequately as soil temperatures increased (Wallace and Romney, 1972). Replacement of ephemeral leaves with perennial leaves of greater diffusion resistance (DuPuit and Caldwell, 1973; Campbell and Harris, 1974) may have restricted the flow

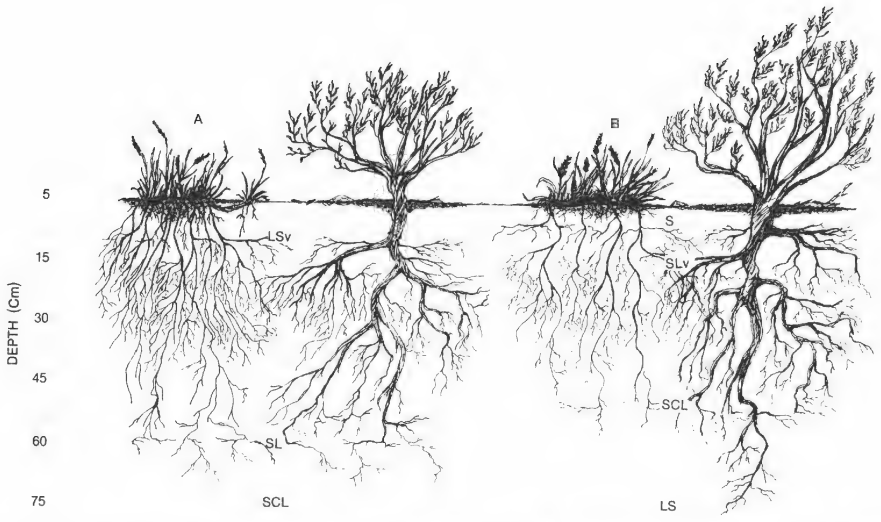


Figure 4. Soil horizons, galleta grass, and rabbitbrush rooting distribution in shadscale (A) and sagebrush (B) communities. S, sand; SL, sandy loam; SCL sandy clay loam; LS, loamy sand; V, vesicular layer.

of water vapor to the thermocouple junction and lowered water potential readings.

Osmotic potentials are low within shadscale plants, and salts are also concentrated within vesicular cells (Caldwell *et al.,* 1972) on the leaf surface. Osmotic water potentials below -200 bars were reported for shadscale when mesophyll tissue and vesicular cells were sampled together (Moore *et al.,* 1972).

The responsiveness of galleta grass and rabbitbrush to summer precipitation contributed to differences in water potentials among species. Halvorson and Patten (1974) also postulated this explanation for variations of plant water potentials in a study of desert species. Water potentials of sagebrush (Hsieh *et al.,* 1971) and shadscale (Moore and Caldwell, 1972) have been shown to respond readily to precipitation in the spring, but to have a substantial lag period following drought (DePuit and Caldwell, 1973).

Water potentials of rabbitbrush in the shadscale community were significantly lower ($P$ 0.1) than those in the upper big sagebrush community. Low water potentials of rabbitbrush plants within the shadscale community are thought to be caused by relatively low soil water potentials during July and August.

Plant water potentials of galleta grass were not significantly ($P$ 0.1) different between communities. Water potentials of rabbitbrush and galleta grass within the same community were significantly different ($P$ 0.1) only when drought or precipitation reduced within-species variation.

*Soil and Plant Water Relations:* Plant water potentials varied with the seasonal progression of soil water potentials and periods of precipitation. Differences between soil and plant water potentials decreased as soil water potentials stabilized between periods of precipitation. After periods of precipitation, soil water potentials declined at a slower rate than plant water potentials and differences between plant and soil water potentials increased.

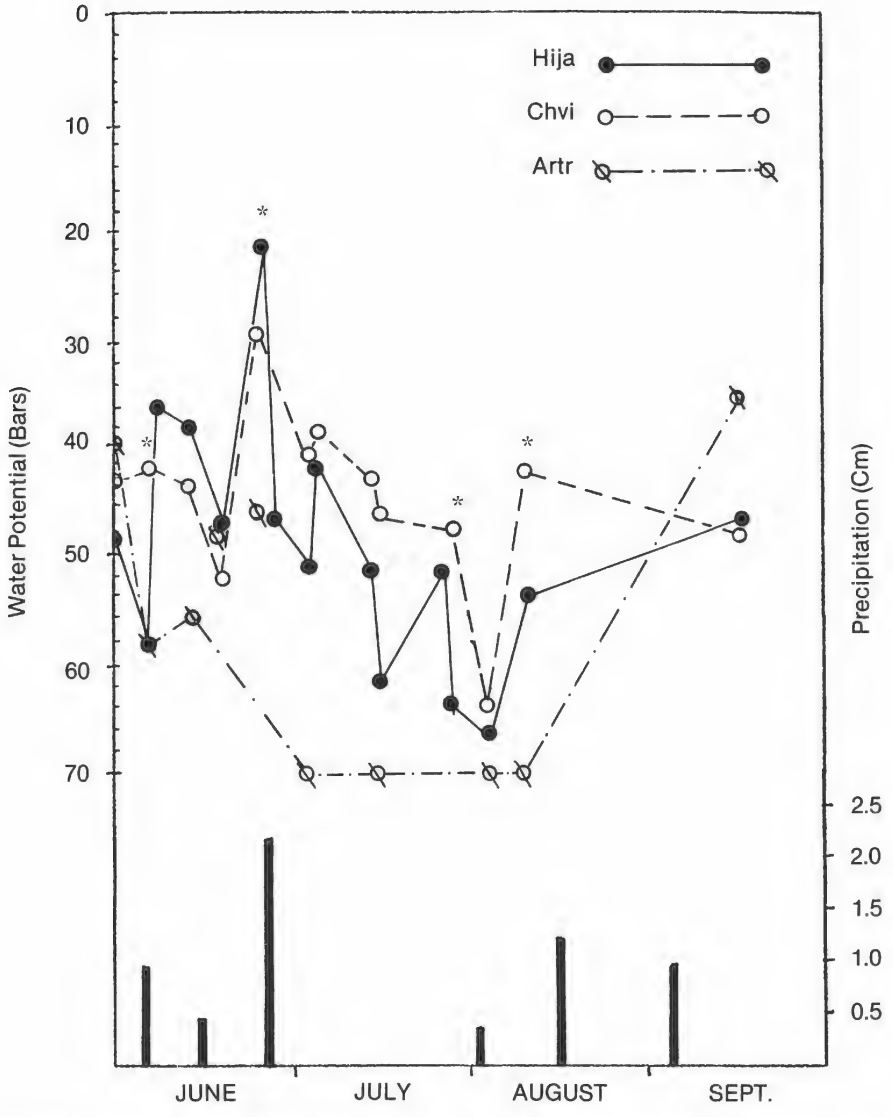


Figure 5. Seasonal patterns in the water potential of galleta grass (Hija), rabbitbrush (Chvi) and big sagebrush (Artr) at the upper big sagebrush community (1972). (*) Denotes a significant difference ($P$ 0.1) in Hija/Chvi water potentials.

**Conclusions**

Variations of water potential among species were caused in part by differences in their physiology and root distribution. Apparently big sagebrush and shadscale plants were physiologically capable of maintaining low water potentials for extended periods of time, but rabbitbrush and galleta grass water potentials reflected current conditions in the

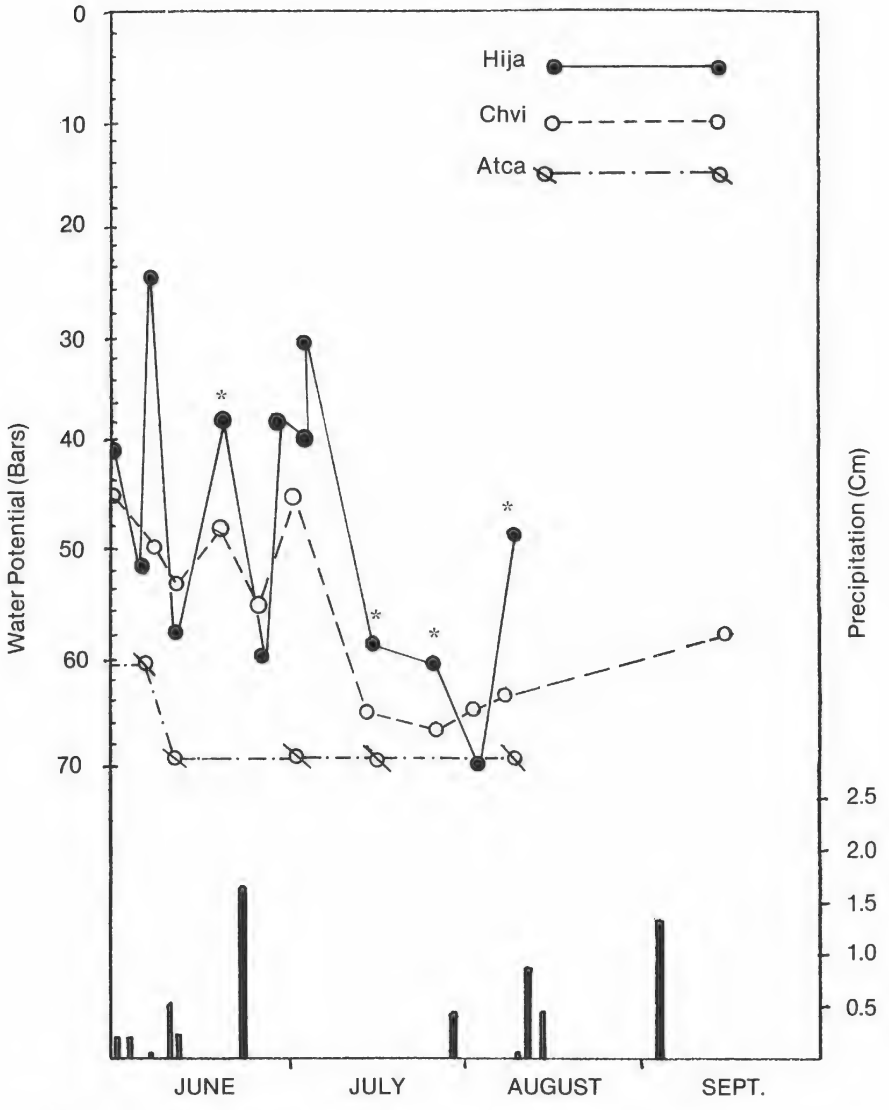


Figure 6. Seasonal patterns in the water potentials of galleta grass (Hija), rabbitbrush (Chvi) and shadscale (Atca) in the shadscale community (1972). (*) Denotes a significant difference ($P$ 0.1) in Hija/Chvi water potentials.

soil-plant system.

Rabbitbrush and galleta grass were apparently able to maintain water potentials above -70 bars through a daily recharge of soil water around the root systems. Early morning soil water gradients indicated water movement into the zone of greatest root concentration in both communities. Soil water withdrawal by absorption and transpiration later in the day perpetuated this water potential gradient.

Water potential gradients within the soil profile appeared selectively to influence water potentials of rabbitbrush and galleta grass. Differences in plant water potential within and between species in the two communities may be partially due to their differential distribution of roots above or below maximum root density and the direction of the water potential gradient within the soil profiles. Root systems which benefit most from water potential gradients within the soil profile could confer an adaptive advantage to the plant. As soil water potential gradients change between sites, different root systems are favored, and a species may become more or less adapted if other factors remain constant.

Adaptation of a species to various sites may be partially inferred from differences in plant water potentials (*i.e.,* rabbitbrush), but only with some skepticism. Until probable range and optimum in water potential for the species is known, the relative importance of such differences remains unclear.

Water potential differences among species do not directly indicate corresponding differences in competitive or adaptive ability. Optimum water potentials necessary for growth, development, and propagation are different for individual species. Insight into adaptive relationships among species may be possible once the optimum water potentials for each species is known, but plant adaptation is much too complex to be determined by water potential alone.

**Acknowledgments**

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# Indicators of Decay in the Grand Fir/White Fir Complex in Central Idaho[1]

## Abstract

We related tree and site characteristics to decay in 1,100 fir trees and found volume loss in a tree could be predicted from increment cores and conks. Volume loss in a stand was related to percentage of trees with external defects, percentage of trees with punky, resinous knots, percentage of trees with conks, and to a lesser extent, to percentage of trees with scars and site moisture. Percentage of trees with decay in a stand was related to percentage of trees with external defects, percentage of trees with punky resinous knots, site moisture, and total basal area.

*Echinodontium tinctorium* Ell. Ev. occurred in more than 97 percent of decayed trees.

We found site moisture and decay incidence were related and could be predicted using understory plant species. Dry sites supported trees with less incidence of decay when compared with moist sites.

## Introduction

The low elevation true fir in central Idaho, known locally as grand fir, *Abies grandis* (Dougl.) Forbes, or white fir, *Abies concolor* (Gord. and Glend) Lindl. constitutes a large proportion of the commercial forests in this region. On the Payette National Forest, this cover type occupies 108,775 acres (44,021 hectares) with a net volume of 1,030,363 MBF (2,431,350 cubic meters).[2] Several authors recognize *A. concolor* as occurring in this region (Davis, 1952; Peck, 1961). Many disclaim its occurrence (McMinn and Maino, 1947; Fowells, 1965; and Little, 1971). This fir population found principally south of the Salmon River has intermediate morphological characteristics ranging between grand fir and white fir and has been recognized as an intergraded complex by Johnson (1966), Daniels (1969), and Frederick (1977). Conversely, Müller (1938), while studying similar fir populations in northeastern Oregon, concluded that morphological similarity to *A. concolor* was due to climatic differences and that there was not real genetic convergence between the two species.

The greatest problem in the management of this fir has been in assessing and predicting the variability and extent of heartrot incidence (Aho, 1974). Defect in merchantable grand fir can vary from practically none to 70 or 80 percent of the stand's

[1]Supported by McIntire-Stennis Funds, U.S. Department of Agriculture.

[2]Personal correspondence with George C. Rhinehart, Timber Management, McCall District, Payette National Forest, June, 1971.

volume (Aho, 1966). Kimmey (1965) has reported volume losses approaching 100 percent in old stands. Young stands of grand fir on certain sites also have considerable heartrot (Hubert, 1955; Maloy and Gross, 1963).

*Echinodontium tinctorium* Ell. and Ev., the Indian paint fungus, causes the greatest amount of heartrot in grand fir (Hubert, 1955; Maloy and Gross, 1963). Other decay fungi isolated from decayed grand fir trees include: *Stereum sanquinolentum* Alb. & Schw. ex Fires, *Pholiota adiposa* Fires, *Odontia bicolor* (Alb. & Schw. ex Fires) Bres., and *Hericium abietis* (Weir ex Hubert) K. Harrison (Hudson, 1972; Maloy, 1968; Maloy and Robinson, 1968). Maloy (1973) reported the absence of *E. tinctorium* in young grand fir trees with advanced decay even though old growth trees in the same stands were infected by the fungus. *E. tinctorium* in the incipient stage destroys the lignin of the heartwood. The infected wood first appears slightly discolored and sometimes water-soaked. This appearance almost disappears when the wood dries, making detection difficult. The rot forms a circular pattern in the trunk and remains confined to the heartwood.

*Infection Courts and Defect Indicators*

*E. tinctorium* has been found to enter grand fir through dead branch stubs (Hubert, 1955), fire scars (Meinecke, 1916), wounds (Maloy, 1973), frost cracks[3] (Aho, 1974; Meinecke, 1916), logging scars, lightning scars, and broken tops (Müller, 1938).

Conks reliably indicate internal decay in grand fir, but the extent of defective wood can vary, depending on conk location, number, aggregation, and size (Aho, 1974; Hubert, 1927; Kimmey, 1965).

Aho (1966) found frost cracks indicated defect in grand fir in the Blue Mountains of Oregon and Washington. Other indicators used to predict internal decay in grand fir have been rusty knots (Hubert, 1927; Kimmey, 1965), tree age, diameter, and presence and number of basal and top injuries (Aho, 1966, 1974). The relative importance of various infection courts and indicators of internal defect is variable and often contradictory. No research evidence exists specifically for the central Idaho fir population.

*Site and Vegetation Relationships*

Certain sites which differ in microclimate from infection-prone areas support grand fir of comparable age and structure with little defect. Weir and Hubert (1918) found more decay in moist, dense, humid river bottom stands than in stands on upland slope sites. Thomas (1955) reported that high average summer temperatures and high humidities together with natural susceptibility and vigor of the host regulate the occurrence and abundance of *E. tinctorium*. Foster *et al.* (1958) found decreased incidence and importance of *E. tinctorium* infections and percentage of total decay with increasing site index. A combination of site conditions seems to favor this fungus, but only site moisture appears consistent.

Understory vegetation can be used to estimate site moisture, but there are few reports relating vegetation and defect in grand fir. Thomas (1955) observed differences in incidence of heartrot in grand fir in coast and inland habitats of British Columbia. Foster *et al.* (1958) found differences in *E. tinctorium* in "fern" and "moss" associations. No reports regarding vegetation-decay relationships exist for central Idaho.

We report here the relationship between site factors, understory vegetation, and

[3]Term used to denote a longitudinal open or closed split in the trunk.

external tree characteristics and the incidence of heartrot decay in the central Idaho grand fir/white fir complex.

### Methods

Stands were located on the Payette and Boise National Forests, on state and private land in west central Idaho. Selected stands showed no recent disturbance as ascertained by visual inspection. We selected stands in various stages of development from poles to mature. These stands occurred on a variety of sites ranging from warm, dry mesic to wet and cool locations. Plot centers were randomly located within selected stands. At each of 110 plots, we extracted, measured, and examined increment cores from 10 grand fir trees. All cores were taken at 4½ ft (1.37 m). A 40 percent grand fir composition was arbitrarily chosen to ensure 10 trees would be present near the plot center within a homogeneous stand. The ten sample trees were selected by taking the largest and smallest diameter trees considered "in" using a B.A.F.-10 prism followed by the two closest trees in each quadrant. Three hundred ninety-eight trees showing incipient or advanced decay in the initial increment boring were bored a second time with a sterilized borer. Cores were saved in sterile tubes for later culturing and identification following the technique of Nobles (1948).

Various individual tree and site data recorded either directly in the field or computed from field data were recorded on marginal punch cards. Some of these key data included: site moisture (1-low to 5-high), understory vegetation (presence and coverage), incidence and number of various defect indicators, and specific defect information.

Fifty-six trees within the 1,100 tree sample were felled, dissected, measured, and examined. These trees were selected on 28 plots most representative of site and stand conditions in the study area. Two trees closest to plot center were selected for felling. The purpose of the dissection was to determine actual volume loss and relate it to various tree and site variables. Previous grand fir decay studies in northern Idaho have shown a strong relationship between the amount of decay in increment cores and volume loss caused by *E. tinctorium* (Partridge, 1972).

In addition to sterilized increment cores, fruiting bodies and decayed wood samples were used to identify fungi from cut trees. Cultures were made from approximately 60 wood samples apparently decayed by *E. tinctorium* to verify field identifications.

Site characteristics of each plot and individual tree attributes were tested in simple and multiple regression analysis to determine if they were related to decay. This testing was done to determine predictors of decay incidence by plot. Also, we predicted volume loss per tree using data from the trees and sites where we dissected trees. From these data, the best volume loss prediction equation was used to predict decay volume loss in the remaining decayed but uncut trees in the study. Extrapolated volume loss estimates on a plot basis were then used as dependent variables and compared in multiple regression with site characteristics. We also expressed decay as the percentage of trees with decay per plot.

We classified each site into one of 5 moisture classes from 1 (dry) to 5 (wet) using site factors recorded in the field. Percent of understory plant coverage (Daubenmire, 1959) was related to each moisture class and compared with the number of trees that were decayed per plot. By establishing site moisture preferences for the understory plants, we classified sites as to probability of decay.

**Results and Discussion**

*Tree and Site Variables*—Multiple regressions used to compare individual tree characteristics of 56 dissected trees with percent volume loss and the volume loss prediction equations are shown in Table 1. More than 70 percent of the variability in decay volume

TABLE 1. Step-wise multiple regression results showing tree characteristics related to the percent volume loss in 56 dissected trees and the volume loss (VL) prediction equations.

| Tree characteristics | Percent volume loss in a tree | | |
|---|---|---|---|
| | $R^2$ | Syx | Sig. |
| A. Percent decay in increment core[1] | 0.5050 | 128.02 | .01 |
| B. Number of conks (1, 2, 3, etc.) per tree | 0.5988 | 116.33 | .01 |
| C. Spiked top (Presence = 1, Absence = 2) | 0.6685 | 106.76 | .01 |
| D. Broken top (Presence = 1, Absence = 2) | 0.7052 | 101.67 | .05 |
| VL[1] = 34.823 + 0.576 A | | | |
| VL = 23.210 + 0.530 + 44.432 B | | | |
| VL = 344.880 + 0.517 A + 50.257 B − 167.407 C | | | |
| VL = 485.666 + 0.543 A + 56.637 B − 176.780 C − 80.974 D | | | |

[1]Percent decay and percent volume loss values = (X 10); e.g., percent decay = 30 = 300 or percent volume loss = 60 = 600.

can be accounted for by four variables, all of which are easily measured or observed. By recording these variables during cruising or marking operations and later entering them into appropriate prediction equations, either by hand or using a computer program, reasonably good estimates of volume loss can be obtained. For example, a fir tree with an increment core showing 20 percent decay (A = 200), one conk on the bole (B = 1), and a spiked top (C = 1) would yield a volume loss of 31 percent. In this case, a broken top is not present (D = 2).

The most consistent predictors of decay on a plot basis using multiple regression were percent of sample trees with punky, resinous knots, with conks, and trees with external defects. Percentage of trees with scars and site moisture also proved useful.

High correlation between these and other independent variables was also found using simple regression. Simple regressions used to compare tree and site characteristics with decay are shown in Table 2. Again, the best predictors of internal defect were the percent of trees with punky, resinous knots and percent of trees with external defects.

Of the total 1,100 trees sampled, 702 were sound, and 398 were decayed. A tree was judged sound if the 16 in increment borer did not strike incipient or advanced decay. The most common indicator on decayed trees was punky, resinous knots which occurred on 255 trees (Table 3). More than 95 percent of these trees had decay. This percentage was surpassed only by total trees with conks, of which 99 percent had decay. Only one tree considered sound had a conk. This conk was located on the upper one-third of the bole and decay had not spread to the butt portion. The small number of sound trees with punky, resinous knots probably were decayed, but either the decay was visually undetectable in the core, or additional borings were needed to detect it.

Eighty-nine percent of trees with scars had decay. Wood decay fungi were not present in most scars caused by recent injuries, but older scars invariably had associated decay. Although grand fir grows fast on most sites, moderate to large scars seldom healed before decay fungi became established.

The preceding three defects reliably indicate decay when they are present. This fact assumes increased importance considering the frequency with which these defects occurred in the sample population.

TABLE 2. Simple linear regression results comparing tree and site variables with the average percent of trees with decay per plot.

| Characteristic of tree or site | Decay<br>Average percent of trees with decay per plot |
|---|---|
| 1. Percent of trees with punky, resinous knots | 0.7450[a]<br>14.28[b]<br>.01[c] |
| Prediction equation | Pd = 10.040 + 1.085X |
| 2. Percent of trees with external defects | 0.7662<br>13.67<br>.01 |
| Prediction equation | Pd = −5.486 + 0.945X |
| 3. Site moisture | 0.5446<br>19.08<br>.01 |
| Prediction equation | Pd − − 6.056 + 15.625X |
| 4. Average stand age | 0.3443<br>22.90<br>.01 |
| Prediction equation | Pd = −33.599 + 0.640X |

[a]$R^2$

[b]Standard deviation

[c]Significance Level: .01 – 99 percent probable

TABLE 3. Various indicators of decay found on grand fir trees in central Idaho.

| Decay indicator | Number of decayed trees with indicator[1] | Number of sound trees with indicator | Percent with indicator and with decay | Percent of total trees with the indicator[1] |
|---|---|---|---|---|
| Scar | 220 | 27 | 89.07 | 22.45 |
| Frost crack | 95 | 42 | 69.34 | 12.45 |
| Punky, resinous knots | 255 | 12 | 95.51 | 24.27 |
| Conks | 130 | 1 | 99.24 | 11.91 |
| Broken top | 39 | 22 | 63.93 | 5.55 |
| Spiked top | 14 | 7 | 66.66 | 1.91 |
| Forked top | 26 | 32 | 44.83 | 5.27 |
| None | 27 | 678 | 3.83 | 64.09 |

[1]More than one indicator frequently was found in a single tree.

Frost cracks did not conclusively indicate decay. Nearly 31 percent of the trees having frost cracks were sound. These cracks appeared frequently on the warm sites, and many were becoming overgrown with new tissues, thus restricting the entrance of pathogenic organisms. The potential infection area of each crack was relatively small, and exposed wood was present for a short time compared with most scars.

Spiked tops and broken tops were fair indicators of decay. These defects occurred on a low percentage of the total sample trees, but when present, approximately two-thirds of the trees were decayed. Many broken tops recorded in the field occurred recently, and decay had not developed. Often these trees were on exposed, windy sites.

Forked tops were the poorest indicators of internal defects. More sound trees had forked tops than did those trees with decay. This finding is not surprising, because this defect often occurred in young stands and nearly always high on the boles. Detection of decay associated with all top indicators was difficult using increment boring at breast height.

*Fungi*

The most common fungus encountered in the examination of 398 decayed trees was *Echinodontium tinctorium* (Table 4). The decay pattern was typically circular, confined to the heartwood, and often left a narrow band of sapwood intact even in advanced cases. The incipient stage was slightly darker than surrounding sound wood and often presented a water-soaked appearance. This latter characteristic was not conclusive evidence of the presence of *E. tinctorium*. Maloy and Gross (1963) reported difficulty in separating incipient decay caused by *E. tinctorium* from wetwood. Hartley *et al.* (1961) related an increase in pH bacteria, and non-hymenomycete fungi to wetwood with no wood deterioration. Several attempts at culturing from water-soaked appearing wood did not yield *E. tinctorium* or any other wood-decaying fungi. Such trees were considered sound.

TABLE 4. Fungi isolated from 398 decayed grand fir trees.

| Fungus | Number[1] | Percent of decayed trees |
|---|---|---|
| *Armillaria mellea* (Vahl.) Quel | 2 | 0.50 |
| *Echinodontium tinctorium* Ell. Ev. | 387 | 97.23 |
| *Fomes roseus* Fr. | 2 | 0.50 |
| *Hericium abietus* (Weir ex Hubert) K. Harrison | 3 | 0.75 |
| *Stereum sulcatum* Burt in Peck. | 2 | 0.50 |
| Various imperfect fungi | 35 | 8.79 |

[1]More than one organism sometimes was present in an individual tree.

*E. tinctorium* was identified in the field by examining the decay pattern, samples of the decayed wood, presence of sporophores, and by culturing using increment cores or samples of the decayed wood. *E. tinctorium* was present with other decay fungi or various imperfect fungi approximately 10 percent of the time.

Association between the root rot-causing fungi, *Fomes nigrolimitatus* (Rom) Egland and *Poria weirii* (Murr.) Murr. in grand fir has been reported by Miller and Partridge (1973). While studying grand fir in northern Idaho, Hudson (1972) found a frequent association between *E. tinctorium* and *Hericium abietus* and *Phialophora fastigiata.*

*Understory Vegetation*

A total of 133 plant species were recorded in this study. The understory plants were recorded on the premise that they may be useful indicators of variable site conditions. Certain plants, by their presence and average coverage values, can be used as indicator species to help identify sites supporting grand fir with a high or low probability of decay. We found incidence and extent of decay related to site moisture conditions. Moist sites supported grand fir which had a higher incidence of decay than did firs growing on drier sites. Plants such as *Calamagrostis rubescens* Buckl. and *Pteridium aquilinum* var. *languinosum* (bong.) Fernald, which were good indicators of dry sites, were also good indicators of low decay incidence (figs. 1 and 3). Correspondingly, species common to sites with high moisture conditions such as *Clintonia uniflora* (Schult.) Knuth., and *Coptis occidentalis* (Nutt.) T. & G. proved to indicate a high percentage of trees with decay (Figs. 2 and 4).

Other workers have reported a relationship between site and heartrot in grand fir.

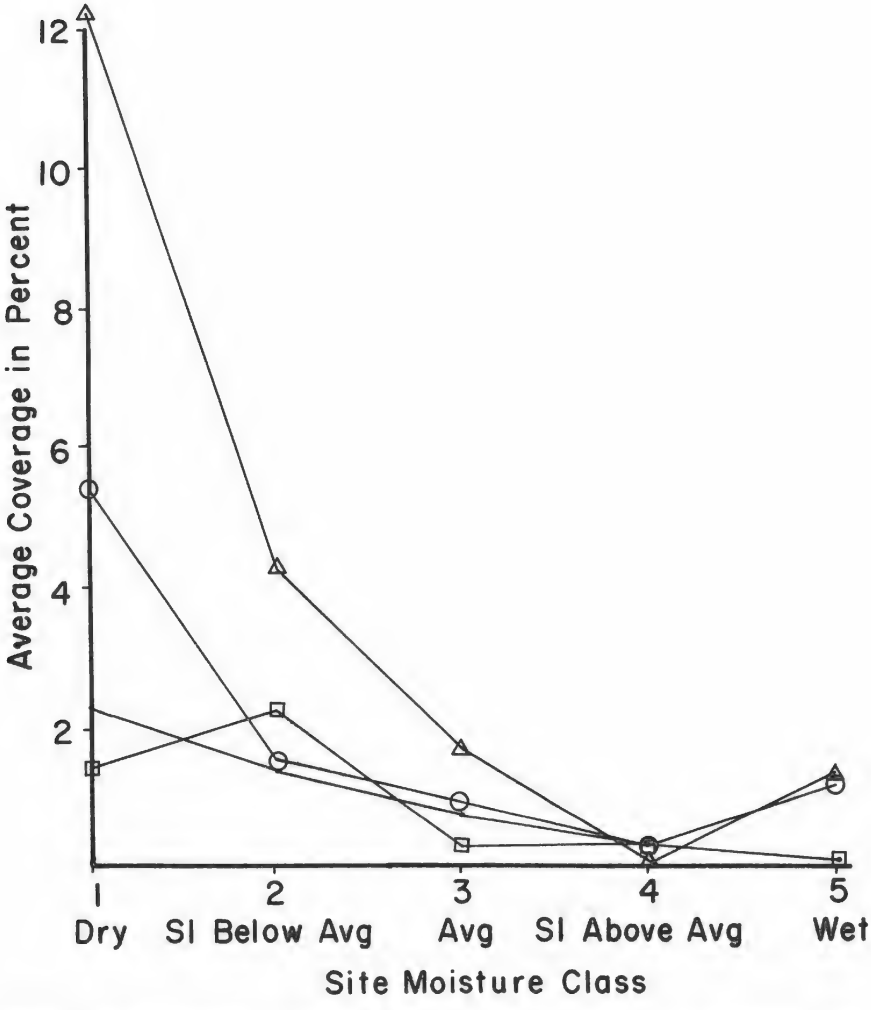


Figure 1. Average coverage in percent of dry site indicator plants related to site moisture classes. Indicator plants are designated by the following symbols: *Calamagrostis rubescens* (—△—), *Symphoricarpos albus* (—□—); *Berberis aquifolium* (—•—) *Pteridium aquilinum* var. *languinosum* (—○—).

Maloy and Robinson (1968) stated that it is not known whether this effect is direct and influences the development of the decay fungi or indirect and alters the susceptibility of grand fir to decay. A proposal advanced by Etheridge, Craig, and Taylor (1971) from their work with *E. tinctorium* in western hemlock involves a microbial factor which affects substrate susceptibility. They speculated that trees growing on the coast of British Columbia were less infected with *E. tinctorium* than trees of the interior because of competing organisms which excluded its establishment. Similar extremes in microclimate may be responsible for differences in grand fir susceptibility from site to site

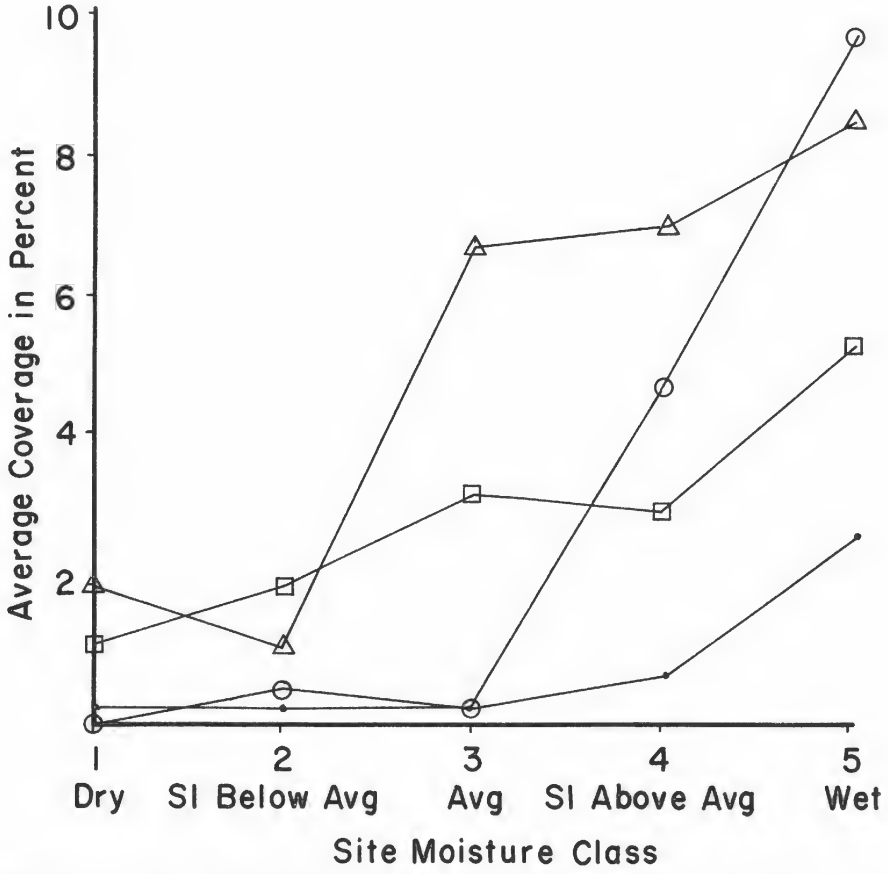


Figure 2. Average coverage in percent of wet site indicator plants related to site moisture classes. Indicator plants are designated by the following symbols: *Clintonia uniflora* (—△—), *Aulacomnium* sp. (—□—), *Cornus stolonifera* var. *occidentalis* (—•—), *Coptis occidentalis* (—O—).

in central Idaho. Evaluating site moisture conditions is necessary for practical applicability. We have attempted to do so, using physical attributes of site and using plant species' composition and coverage.

We found grand fir occurring as a climax tree throughout the study area on diverse sites. From the vegetation data, we suggest the grand fir zone in this region of Idaho could be divided into two habitat types: a dry phase grand fir—*Calamagrostis rubescens* or *Symphoricarpos albus* (L.) Blake; and a wet phase grand fir—*Coptis occidentalis* or *Clintonia uniflora.* Either phase is characterized by grand fir in all stages of development, but the understory plant composition and coverages are different. The dry phase is characterized by the presence of some or all of the following species: *Calamagrostis rubescens, Symphoricarpos albus, Pteridium aquilinum* var. *languinosum,* and *Berberis aquifolium* Pursh. (Figs. 1 and 3). The wet phase is characterized by *C. uniflora, C.*

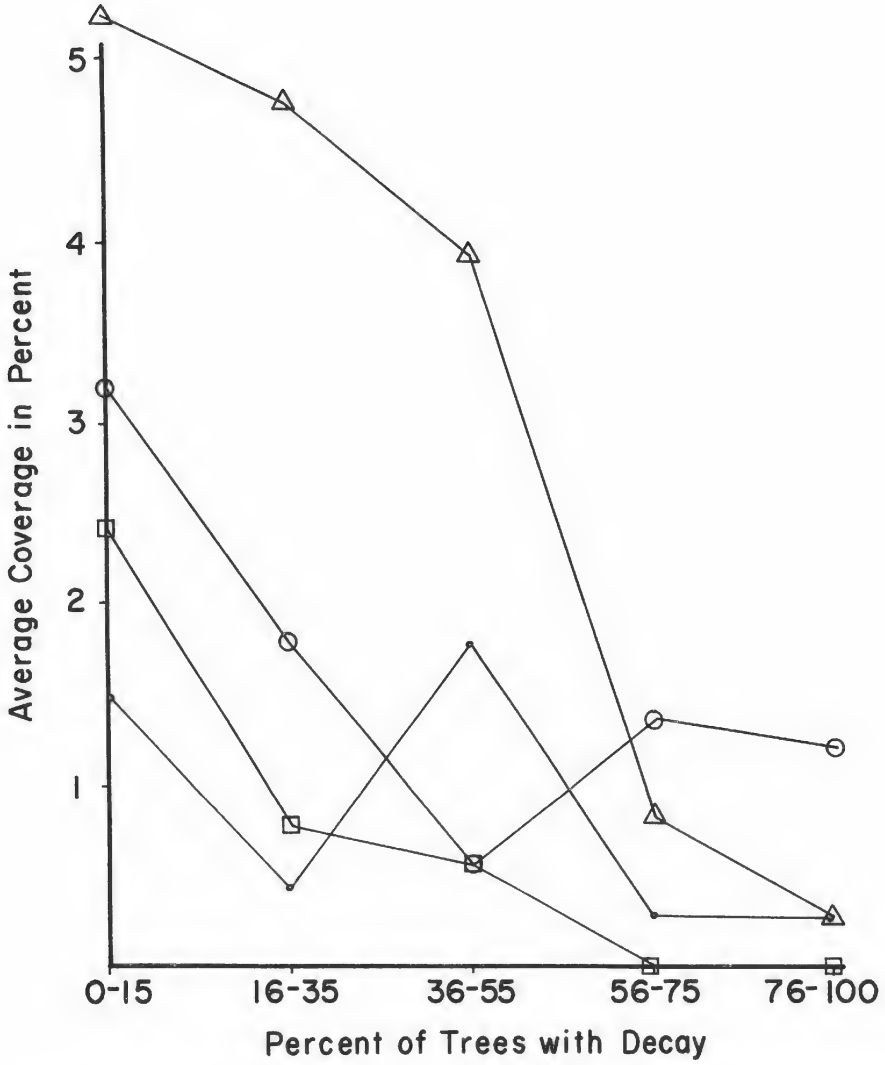


Figure 3. Average coverage in percent of low grand fir decay indicator plants related to average percent of trees with decay per plot. Indicator plants are designated by the following symbols: *Calamagrostis rubescens* (-△-), *Symphoricarpos albus* (-□-), *Berberis aquilinum* (—•—), *Pteridium aquilinum* var. *languinosum* (-○-).

*occidentalis, Cornus stolonifera* var. *occidentalis* T. & G., and *Aulacomnium* sp. (Figs. 2 and 4). Dry site indicator species are absent in the wet phase association or when present exhibit low average coverage values. The opposite is evident when the wet phase is considered.

Because full expression of site conditions by plants takes many years, seral stands

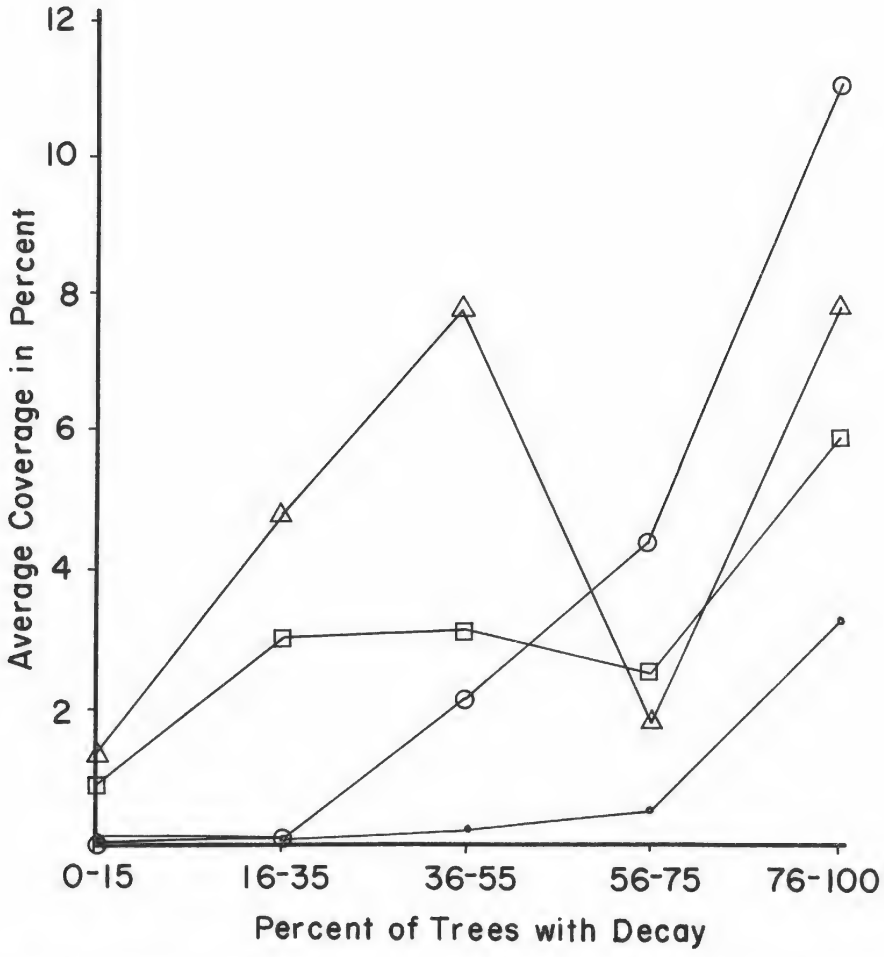


Figure 4. Average coverage in percent of high grand fir decay indicator plants related to average percent of trees with decay per plot. Indicator plants are designated by the following symbols: *Clintonia uniflora* (—△—), *Aulacomnium* sp. (—□—), *Cornus stolonifera* var. *occidentalis* (—•—), *Coptis occidentalis* (—○—).

may vary from the above classification. For example, dry-site-indicator species may temporarily be found on sites which at a later successional stage would not support them.

The results and conclusions of this study are for a specific region having unique characteristics and therefore may not be applicable to other areas without modification. However, these findings can provide a base for better understanding decay relationships in other true fir populations of the region.

**Acknowledgments**

Thanks are extended to Dr. Rexford Daubenmire, Washington State University, for his suggestions in the early developmental stages of this study.

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# Feral Rabbits on San Juan Island, Washington

**Abstract**

A survey of the rabbit distribution on San Juan Island, Washington, using several methods, showed a gradient from plentiful at the southern end to few or no rabbits at the northern end. This gradient is caused by a combination of vegetation, soils, and rainfall. A shot sample of rabbits showed their body and organ weights and litter size to be higher than those of rabbits from other feral populations around the world. There appear to be few predators, and land use patterns favor the continued existence of the rabbit on the Island.

The first report of feral rabbits, *Oryctolagus cuniculus,* on San Juan Island appears to be that of Couch (1929). There have been several other articles since, but they all have been in relation to the introduction of the "San Juan rabbit" to the U.S. mainland (e.g., Latham, 1955; Thompsen, 1955; Kirkpatrick, 1959).

The purpose of this note is to present contemporary data on the feral rabbits on San Juan Island.

San Juan Island lies adjacent to the U.S.A./Canadian border near Vancouver; it is approximately 22 km long and has a maximum width of 10 km near the center.

The Island has a temperate climate with cool, dry summers and mild, moist winters. Rainfall varies from 740 mm at Roche Harbor (northern end) to 48 mm per year at Cattle Point (southern end). The soils on San Juan are glaciated tills, varying from well-drained at Cattle Point to poorly drained in the middle and northern parts of the Island (data from Schlots *et al.,* 1962).

There is a distinct gradient from medium to dense stands of conifers, often with thick ground cover, at the northern end of San Juan to open pastures and grasslands with clumps of conifers and deciduous trees and hedgerows at the southern end.

A map of the Island showing areas of timber and open grassland was drawn from aerial photographs (Figure 1a).

*Distribution of rabbits.* The distribution of rabbits on the Island is shown in Figure 1b. The map is compiled from the results of a survey carried out in November, 1968, and May-June, 1969. Evidence of rabbits is based on the presence of burrows and indications of their current use (e.g., fresh digging), the presence of fresh feces on dung hills, and the numbers of rabbits, both alive and dead, observed on roads around the Island.

Rabbit numbers vary from plentiful at the southern end of the Island to none or very few at the northern end, and in general are restricted to the well-drained soils in areas cleared for farming. Burrows in these soils are dry in early summer and hence

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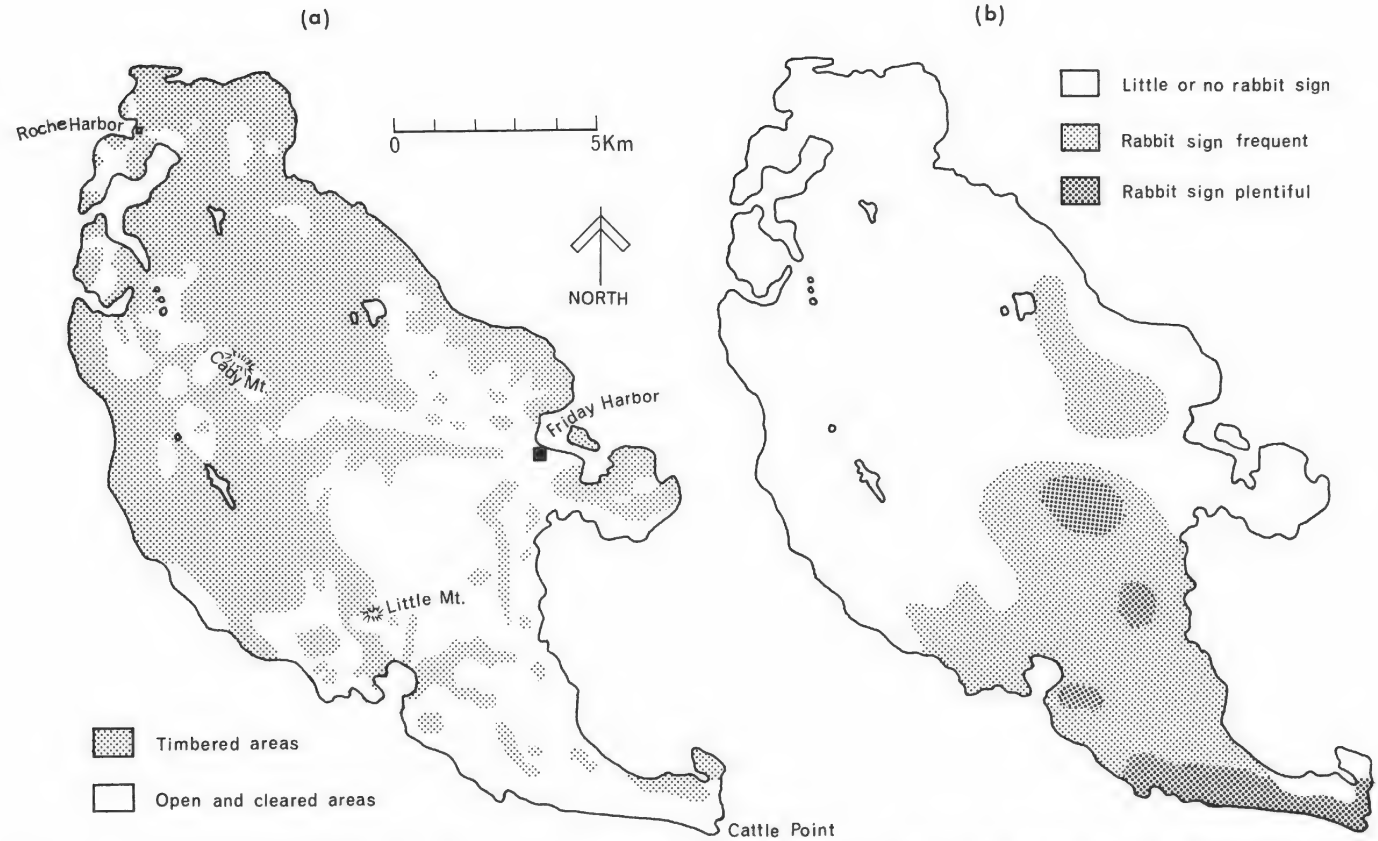


Figure 1. (a) Distribution of timbered, open, and cleared land on San Juan Island. (b) Rabbit distribution on San Juan Island.

favor the survival of nestling rabbits which are adversely affected by dampness (Myers and Poole, 1963).

Hedgerows and patches of brush in cleared areas are utilized by rabbits as shelter from predators, and as resting places during winter months when burrows are damp.

Areas that are heavily timbered or have poorly drained soils support very few rabbits.

*General biology.* A sample of 38 rabbits was collected at the southern end of the Island between June 19 and 28, 1969. Data on sex, body weight, ear length, weights of adrenal glands and reproductive organs were collected from each individual.

The sample was divided into two age-groups by plotting body weight against eye lens weight. Two groups were apparent, those with a heavy body weight/eye lens weight (adults), and a group with much lighter weights (juveniles) (Myers and Gilbert, 1968).

The mean adult body weight for both sexes is significantly larger than body weights of adult rabbits collected from several areas in Australia, England, and New Zealand (Table 1). The large body weight of the San Juan Island rabbit has been recorded

TABLE 1. Comparative body weights of rabbits from different localities.

| Locality | Mean Body Weight (g) Male | Female |
|---|---|---|
| San Juan Island | 2162 | 2414 |
| Australia* | 1304 | 1540 |
| New Zealand[a] | 1559 | 1796 |
| England[b] | 1416-1465 | 1404-1453 |

*Myers (1970, and unpubl.)
[a]Wodzicki and Darwin (1962).
[b]Stephens (1952).

previously (Latham, 1955; Thomsen and Evans, 1964). The ears of the sample rabbits are longer than those in Australian rabbits. Large ears are a characteristic of several domestic breeds, including the "Belgian hare," which was one of the first breeds of the domestic rabbit to have been released on San Juan (Couch, 1929).

The predominant coat color in the San Juan rabbits is agouti (36/38), suggesting that the rabbits may be reverting to wild type, but retaining the large body size and ears of domestic breeds.

The organ weights of the adults are also heavy when compared with Australian rabbits (Myers, 1970). Adult males have a particularly heavy spleen (mean 1.1 gm), indicating the possibility of some kind of physiological stress.

The smallest female to show reproductive activity weighed 1,500 gm. This figure contrasts with a body weight of 1,000 gm (3 months old) recorded in Australian rabbits by Myers and Poole (1962) and Dunsmore (1971).

The litter size as indicated by corpora lutea numbers had a mean of 7.3, which is much larger than that of any known wild rabbit population. In Australia, the mean litter size varies between 4.49 and 5.65 (Myers, 1970); in New Zealand, litters average 6.70 (Wodzicki and Darwin, 1962); and in Wales, 4.36 (Stephens, 1952). Two adult females in the sample showed evidence of resorbed embryos and no new ovulations, suggesting that their breeding season had ended.

The heavy body weights of the juvenile females indicate a fast growth rate, further evidence of their domestic ancestry.

*Predators.* The red fox, *Vulpes vulpes,* was released by local inhabitants on San Juan Island in 1963 and again in 1965, presumably to help control rabbits. Several fox scats found at Cattle Point contained claws of the horned lark, *Otocoris alpestris,* small mammal bones, and short fur (8 mm). On San Juan the fox does not appear to excavate rabbit burrows containing nestling young, as it does in Australia and Europe.

Both the golden eagle, *Aquila chrysaetos,* and bald eagle, *Haliaeetus leucocephalus,* were observed on numerous occasions feeding on rabbit carcasses. Apparently most of these rabbits had been killed by automobiles. Retfalvi (1970) points out that these dead rabbits are an important food source for the bald eagle on San Juan Island.

A sharp-shinned hawk, *Accipiter striatus,* was observed with part of a freshly killed rabbit kitten near Eagle Point in May, 1969.

Human activities constitute one of the main mortality factors for the rabbits on San Juan Island. Although the shipping of rabbits and their carcasses from San Juan Island has fallen off considerably in the last few years, there is still regular netting (catching) and shooting of rabbits on the Island. Attempts to control rabbit numbers by poisoning appear to have had little effect.

*Current situation.* The successful maintenance of numbers by the European rabbit on San Juan Island is probably attributable to several factors—(a) the Island has a Mediterranean-type climate and the well-drained soils at the southern end of the Island are suited for rabbit burrows; (b) the Island has cleared, well-grazed areas which provide favorable feeding areas for rabbits; (c) hedgerows and patches of brush provide protection from predators and additional cover for rabbits; and (d) there is no rabbit predator of any consequence on the Island.

**Acknowledgments**

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## Association News

The annual fall meeting of Officers and Trustees was held in Ellensburg, Washington, on October 22, 1977, with fourteen members in attendance. Reports of the Secretary and Treasurer indicate the business of the Association to be in order and the Association to be financially sound. The journal editor reported his plan to publish two double issues in 1978 to reduce the backlog of manuscripts which now exists.

President Otis Maloy announced the resignation of Vice President W. L. Barrett which was accepted with regret. Dr. Ronald J. Taylor was named his successor.

An important action taken by the Trustees was to prepare an amendment to the Constitution that establishes a method for replacement of officers when an office is vacated during a term. The amendment is included here for your information and will be voted on at the annual meeting in March, 1978.

The Trustees voted to put a dues increase before the Association at the March, 1978, meeting. The proposed schedule of dues is as follows:

| | | | |
|---|---|---|---|
| Sustaining Individual Member | $20.00 | Institutions with 3000 and more students remain at | 30.00 |
| Regular Member | 10.00 | Sustaining Corporation will remain at | 50.00 |
| Student Member | 5.00 | | |
| Institutions with less than 3000 students | 20.00 | | |

These recommended increases are to fight inflation and cover part of the increased costs of the journal, particularly those costs involved with publishing 1978's extra issues. These dues would start in January, 1979.

President Maloy reported that the 1978 meeting plans for March 30, 31, and April 1 at Washington State University in Pullman are progressing on schedule. Bob Jonas is Local Arrangements Chairman and Dave Baumgartner is Program Chairman. A symposium on Science Education in Society is being planned by Glenn Crosby.
Section Chairpersons are as follows:

| | | | |
|---|---|---|---|
| Botany | William R. Rayburn, WSU | Social Service | Nancy Hultquist, U of I |
| Forestry | Donald R. Satterlund, WSU | Soil & Water | Donald L. Johnstone, WSU |
| Geology | Joseph W. Mills, WSU | Zoology | John M. Larsen, Jr., WSU |
| Science Educ., Math | Glenn A. Crosby, WSU | Chemistry-Physics | A. Keith Dunker, WSU |

Proposed amendment to the Constitution which will become part of Article IV, entitled "Officers," is:

"Vacancy of the office of President is filled by advancement of the Vice-President. Replacements for vacancies in other offices shall be appointed by the President."

Milton M. Mosher, Secretary

**Northwest Science**

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Adolph Hecht, Editor

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